Tundra Species Diversity and Plant Traits in a Changing Arctic

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“If at first you don’t succeed, try, try, try again.”

(English proverb)

Global air temperature is unequivocally increasing and will keep rising, more rapidly in the Arctic than in other regions. Climate warming may affect not only soil factors, e.g. temperature, moisture and nutrient availability for plants, but also vegetation. Changes in species diversity, distribution, and plant traits are expected as a consequence of direct and indirect effects of climate warming, especially in high-latitude ecosystems. Two of the main changes expected in arctic tundra are shrub expansion and loss of cryptogam diversity. Tundra vegetation shifts will result in altered feedbacks with atmosphere and permafrost through the surface energy budget and the water and carbon cycle, which might affect regional climate. Despite the high vulnerability of arctic species to climate change and the importance of tundra vegetation–climate feedbacks, uncertainties remain in relation to species diversity and plant trait response to climate.

In order to identify changes in species diversity, community composition, and plant traits that might take place under climate change in arctic tundra ecosystems, I combined observational, experimental, and dendroecological approaches. I established a set of observational plots in two contrasting habitats in northeastern Siberia, finding that species diversity and community composition were closely related to edaphic factors. These relationships were different among plant functional types, suggesting a higher vulnerability of cryptogam diversity to changes in edaphic factors and, therefore, to climate warming. Moreover, by sampling shrub individuals from experimental soil warming and fertilization plots, I found faster shrub growth with enhanced nutrient availability, a decrease in bark investment with faster growth rates, and a coordinated response of shrub traits to nutrient addition. These findings suggest a shift in growth strategy and resource acquisition towards more rapid ones with climate warming. Although shrub expansion is expected in the short term due to faster growth and denser covers, in the long term, shrubs might become more vulnerable to herbivory, pathogens, and climate extremes because of shifts in shrub resource allocation towards growth (growth–defence trade-off).

This thesis contributes, therefore, to increase our knowledge of species diversity vulnerability and plant trait shifts in a changing Arctic, which is a first step to better understand vegetation effects on the surface radiation budget in tundra ecosystems. Such an understanding is essential for reducing the uncertainties in direction and magnitude of future vegetation–climate feedbacks.

Die globale Lufttemperatur steigt erwiesenermassen an und wird sich auch weiterhin erhöhen. Diese Erwärmung schreitet in der Arktis noch schneller fort als in anderen Regionen. Die Klimaerwärmung beeinflusst nicht nur Bodenfaktoren, wie Temperatur, Feuchtigkeits und Nährstoffverfügbarkeit für Pflanzen, sondern auch die Vegetation. Als direkte und indirekte Folgen der Klimaerwärmung werden Veränderungen in der Artenvielfalt, der räumlichen Verteilung der Arten und der Pflanzeneigenschaften erwartet, insbesondere in Ökosystemen im hohen Norden. Zwei besonders wichtige mögliche Veränderungen in der arktischen Tundra sind die Ausbreitung von Sträuchern und der Verlust von Diversität bei Kryptogamen. Veränderungen in der Tundrenvegetation werden die Wechselwirkungen mit der Atmosphäre und dem Permafrost beeinflussen, über den Energiehaushalt an der Oberfläche, sowie den Wasser- und Kohlenstoffkreislauf, mit Auswirkungen auf das regionale Klima. Trotz hoher Empfindlichkeit arktischer Arten auf den Klimawandel und der Bedeutung der Wechselwirkungen zwischen Tundrenvegetation und Klima bleiben Unsicherheiten bestehen bezüglich der Reaktion der Artenvielfalt und Pflanzeneigenschaften auf die Klimaveränderung.

Um die Veränderungen der Artenvielfalt, der Zusammensetzung der Pflanzengesellschaften und der Pflanzeneigenschaften auf den Klimawandel in arktischen Tundra-Ökosystemen zu identifizieren, kombinierte ich beobachtende, experimentelle und dendrochronologische Vorgehensweisen. Ich etablierte Beobachtungsflächen in zwei unterschiedlichen Habitaten in Nordostsibirien und fand heraus, dass die Artenvielfalt und die Zusammensetzung der Pflanzengesellschaft in einer engen Beziehung zu den Bodenfaktoren standen. Diese Beziehungen unterschieden sich zwischen den funktionellen Gruppen, was auf eine stärkere Empfindlichkeit der Diversität von Kryptogamen auf Änderungen der Bodenfaktoren und damit auf die Klimaerwärmung hindeutet. Bei der Beprobung von Sträuchern auf experimentellen Flächen mit Bodenerwärmung und Düngerzufuhr fand ich schnelleres Strauchwachstum, eine verringerte Investition in die Rinde, sowie eine koordinierte Reaktion der Straucheigenschaften auf gedüngten Flächen. Diese Ergebnisse deuten auf eine Verlagerung der Pflanzenstrategien unter fortschreitender Klimaerwärmung hin, in Richtung eines schnelleren Wachstums und veränderten Trade-offs in der Ressourcenaufnahme. Obwohl durch das schnellere Wachstum und die dichtere Pflanzendecke kurzfristig eine Ausbreitung von Sträuchern zu erwarten ist, könnten Sträucher langfristig empfindlicher gegenüber Herbivorie, Krankheitserregern und Klimaextremen werden, da sie ihre Ressourcen verstärkt in das Wachstum investieren anstatt in die Abwehr (Wachstum–Abwehr Trade-off).

Die vorliegende Arbeit trägt dazu bei, unser Wissen zur Artenvielfalt, zur Vulnerabilität und zu Verschiebungen der Pflanzeneigenschaften in einer sich verändernden Arktis zu erweitern. Dies ist ein erster Schritt, um den Einfluss der Vegetation auf den Energiehaushalt an der Oberfläche in Tundra-Ökosystemen besser zu verstehen. Dieses Verständnis ist notwendig, um die Unsicherheiten betreffend der Richtung und Grösse der zukünftigen Wechselwirkungen zwischen Vegetation und Klima zu reduzieren.

CHAPTER 1

General introduction

"It is virtually impossible to understand how biology works

outside of the context of environment."

(Robert Sapolsky Maurice)

1.1 Background

1.1.1 Climate change in the Arctic

Global air temperature is unequivocally increasing (+0.8°C over the period 1880 to 2012) and is expected to keep rising (+1.5°C by the end of this century; emission scenario RCP4.5; IPCC, 2013). In the Arctic, surface air temperature has risen more rapidly than in other regions over the past decades and is projected to increase by around 3°C (RCP4.5; IPCC, 2013). This Arctic amplification is suggested to be driven by temperature feedbacks – more energy radiated to space as the surface warms in low than high latitudes mainly due to different vertical structure of the warming – and surface albedo feedbacks – increased surface absorption of solar radiation because of snow cover reduction and ice retreat (Pithan & Mauritsen 2014). In addition to climate warming, changes in precipitation, soil moisture, and cloud and snow cover among others are projected over the 21st century. For example, an increase in precipitation (20%; RCP4.5) and a decrease in snow cover and permafrost thickness are expected in the Arctic (IPCC, 2013).

1.1.2 Tundra plant traits and strategies

Harsh environmental conditions (e.g. extremely low temperatures, scarce precipitation), poorly developed soils, active cryogenic processes, and short growing seasons (< 3 months) characterize high-latitude ecosystems (Billings & Mooney 1968; Chernov & Matveyeva 1997; Walker 2000). Tundra vegetation is adapted to these conditions, which is reflected in their plant traits (e.g. low height, long leaf life-span, and small thick leaves), slow growth rates, and high persistence of nutrients (Shaver & Chapin 1980; Reich, Walters & Ellsworth 1997; Cornelissen 1999). This conservative strategy – low rates of resource acquisition, tissue turnover, and growth – allows tundra species to allocate resources to other processes, such as defence against pathogens or storage, conferring plants stress resistance (Chapin, Autumn & Pugnaire 1993). Conservative strategies are advantageous under low-resource conditions (Chapin *et al.* 1993; Reich 2014). However, these strategies can be a disadvantage under higher-resource conditions, like the ones expected with climate change, because slow-growing species can be outcompeted (e.g. through light) by species with faster growth (Reich 2014).

1.1.3 Shrub expansion and tundra diversity

Shrub expansion has been reported in many arctic regions using long-term monitoring plots, repeat aerial photography, and satellite imagery (Tape, Sturm & Racine 2006; Forbes, Fauria & Zetterberg 2010; Myers-Smith *et al.* 2011; Frost & Epstein 2014). The expansion, which is suggested to be driven by climate warming, can take place by recruitment between existing patches, colonization of new areas, and lateral and vertical growth (Tape *et al.* 2006; Myers-Smith *et al.* 2011). However, arctic shrub expansion is spatially and temporally heterogeneous, that can be attributed to different shrub growth strategies and sensitivity to climate, in addition to the high variation of environmental conditions across the Arctic (Myers-Smith *et al.* 2011; Elmendorf *et al.* 2012).

Shrub expansion may affect negatively other tundra species, mainly cryptogams (bryophytes and lichens), by outcompeting those species for light (e.g. cover shading, litter deposition) and resources or varying local soil conditions (Cornelissen *et al.* 2001; Sedia & Ehrenfeld 2003; van der Wal *et al.* 2005; Odland, Reinhardt & Pedersen 2015). Cryptogams, which account for most of tundra species diversity, might decline or even disappear as a consequence of shrub expansion, decreasing the species diversity on these ecosystems (Cornelissen *et al.* 2001).

1.1.4 Tundra vegetation–climate feedbacks

Climate warming can cause changes in vegetation composition, diversity, and distribution through direct and indirect effects like increased mineral nutrient availability for plants as a result of higher organic matter mineralization rates (Epstein et al., 2000; Schmidt et al., 1999; Walther et al., 2002). Furthermore, climate change may also affect soil characteristics through increased soil temperature, fluctuations in moisture, and enhanced nutrient availability (IPCC, 2013; Keller et al., 2004; Seneviratne et al., 2010). As community assembly is driven by biotic and abiotic interactions, additional changes in species composition and diversity are expected (Cornwell and Ackerly, 2009).

Vegetation species both respond to and influence local climate and soil characteristics (Medinski et al., 2010; Valladares et al., 2015; van der Putten et al., 2013). Therefore, vegetation shifts projected for the Arctic may result in altered feedbacks among vegetation, atmosphere, and permafrost, which might in turn affect climate (Beringer et al., 2005b; Chapin et al., 1996). In case of shrub expansion, the surface energy budget and the water and carbon cycles can be altered through shifts in community composition and species diversity (indirect effects) or

denser shrub cover, plant trait changes, and greater woody surface (direct effects) (Eugster et al., 2000; Juszak et al., 2016). For example, summer permafrost thaw decreases with higher shrub cover through soil shading (Blok et al., 2010; Nauta et al., 2015), but this protection might be lower than the thermal insulation provided by the cryptogam layer. Moreover, increased shrub biomass and cover may reduce the canopy albedo and, therefore, increase the net surface radiation (Beringer et al., 2005b; Blok et al., 2011; Thompson et al., 2004). Additionally, greater woody surface and changing leaf to wood ratio will have effects on surface albedo, but also on carbon uptake by shrubs. Vegetation shifts may also affect important ecosystem processes such as biomass production or litter decomposition (Balvanera et al., 2006; Cardinale et al., 2011; Hector et al., 1999).

Those are only a few examples of tundra interactions with climate. Feedbacks are numerous and complex, many of them still uncertain in terms of direction and magnitude (Elmendorf et al., 2012; Myers-Smith et al., 2011). Identifying the relationships between species diversity and environmental factors and the potential responses of plant traits to future environmental conditions is important for predicting tundra vegetation shifts and ecosystem processes in a changing climate.

1.2 Study area and vegetation

The study area is located in the Yakutian nature reserve of Kytalyk, northeastern Siberia (70°49'N, 147°28'E, 10 m.a.s.l.), in the continuous permafrost arctic region (Fig. 1.1). The mean annual air temperature is -13.1°C with minimum and maximum monthly means of -33.5°C in January and 11.2°C in July and the mean annual precipitation is 210 mm (1980–2013, WMO station 21946, Chokurdakh, monthly summaries of GHCN-D, NOAA National Climatic Data Center). Three geomorphological units are present at the study area: a Pleistocene yedoma hill, an alas (Fig. 1.2) – hereinafter referred to as ridge and lakebed – and a flood plain (Schirrmeister *et al.*, 2012). Two cryogenic relief-forms are typical on the lakebed: low- and high-centred polygonal complexes. In the high-centred polygonal complex, wet hollows alternate with elevated polygons, which are higher and better drained. The main vegetation present in the area is tussock sedge tundra with abundant dwarf shrubs on the ridge and, on the lakebed, sedge wetlands in the hollows and dwarf birch-moss communities on the polygons; high willow copses are characteristic for the flood plain (Iturrate-Garcia *et al.*, 2016).

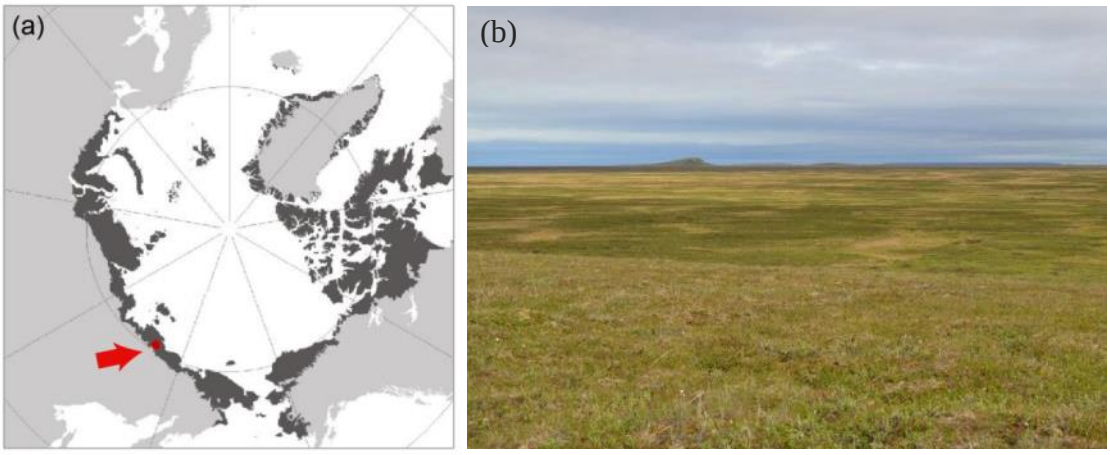

Figure 1.1: (a) Location of the study area (red point); in dark grey, extent of Arctic tundra (data from Walker *et al.* 2005); (b) photograph of the study area landscape.

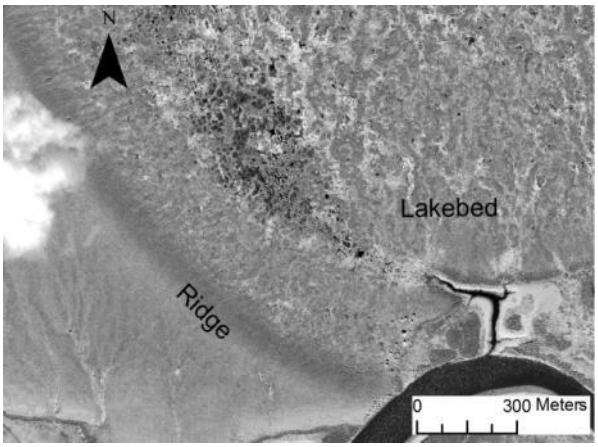

Figure 1.2: Locations of the ridge and lakebed. The figure background is a GeoEye-1satellite image (August 2010).

Four main tundra vegetation types were considered (Fig. 1.3) in Chapter 2, following the classification of the circumpolar arctic vegetation map (Walker 2000).

- Tussock sedge, dwarf shrub, moss tundra (G4): moist tundra of low height (< 25 cm), dominated by the sedge *Eriophorum vaginatum* and deciduous and evergreen dwarf shrubs (mainly *Betula nana, Dryas octopetala, Ledum palustre,* and *Vaccinium vitis-idaea*) with abundant mosses *(Aulacomnium* spp., *Dicranum* spp., *Hylocomnium splendes,* and *Tomentypnum nitens*).

- Erect dwarf shrub tundra (S1): moist to dry tundra (15-30 cm height) dominated by *Betula nana* and mosses with rather abundant grasses (*Calamagrostis holmii)* and lichens (*Cetraria islandica* and *Flavocetraria cucculata*).

- Sedge, moss, dwarf shrub wetland (W2): wetland complexes with a canopy height around 40 cm, dominated by sedges (*Eriophorum angustifolium)* and mosses (*Sphagnum* spp.), but including dwarf shrubs (*Betula nana* and *Salix pulchra).*

- Dwarf shrub, lichen tundra (S1.2): moist tundra (< 5 cm) in the transition areas between S1 and W2, dominated by the evergreen dwarf shrub *Vaccinium vitis-idaea* and lichens (mainly *Flavocetraria cucculata*). Scarce cover of *Betula nana* and mosses are present when the area is closer to S1.

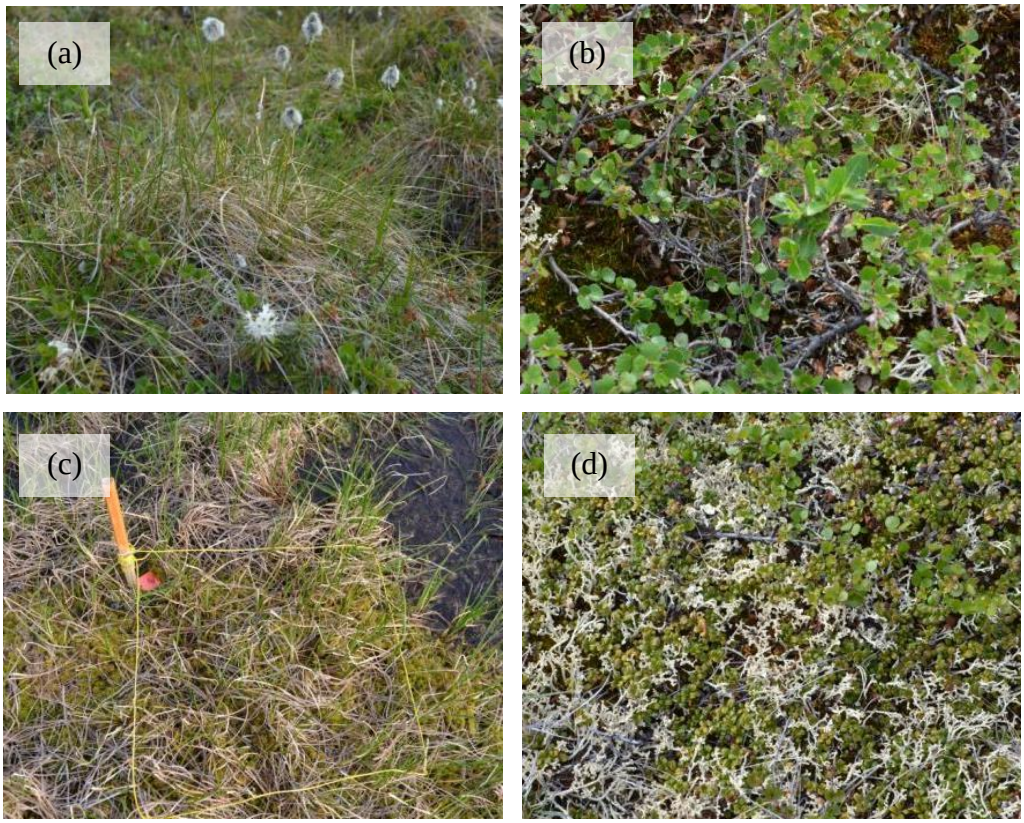

Figure 1.3: Study vegetation types: tussock-sedge, dwarf shrub, moss tundra (a); erect dwarf shrub tundra (b); sedge, moss, dwarf shrub wetland (c); dwarf shrub, lichen tundra (d).

In Chapters 3 and 4, I focused on four shrub species dominant in the study area: *Betula nana* ssp. *exilis* (Sukazcev) Hultén, *Ledum palustre* ssp. *decumbens* (Aiton) Hultén, *Salix pulchra* Cham., and *Vaccinium vitis-idaea* L. (Fig. 1.4). Tundra shrubs are defined as woody perennial plants of stature lower than 2 m that produce several stems in their base instead of a single trunk; low shrubs are shrubs between 0.4 and 2 m tall and dwarf shrubs lower than 0.4 m, that is further divided into erect (0.1-0.4 m with erect stems) and prostrate dwarf shrubs (< 0.1 m with stems developing laterally along the ground) (Myers-Smith *et al.* 2011).

- *Betula nana* (Betulaceae) is a deciduous erect dwarf-shrub lower than 40 cm that occurs on moist, acidic, and nutrient-poor sites, but also on well-drained areas (Whittaker 1993). Rhizomes and roots (ecomycorrhizal) account for 80% total plant biomass (Chapin 1980b). This species reproduces by seeds and, most commonly, by branch layering and sprouting (Hultén 1968). It is shade intolerant (Chapin & Shaver 1985).

- *Ledum palustre* (Ericaceae) is an evergreen prostrate dwarf-shrub. Less than 50% total biomass is underground (Chapin 1980b). The slow growth rate and nutrient tissue turnover allows this species to grow in low nutrient environments with slightly acid soils (Chapin & Shaver 1996). Soil nutrients are transferred to the leaves, becoming storage organs during the winter (Chapin, Johnson & Mckendrick 1980). Its reproduction is by seed production or vegetative sprouting, which predominates in disturbed communities (Chapin & Shaver 1996). It is shade tolerant (Chapin & Shaver 1985).

- *Salix pulchra* (Salicaceae) is a deciduous low-shrub (~ 2 m on river banks), but in tussock tundra can be considered erect dwarf-shrub (< 40 cm). It has the highest covers in areas with shallow, perched water tables (Dyrnes *et al.*, 1979). The main mode of reproduction of this species is by seeds (Hultén 1968). It is shade intolerant (Chapin & Shaver 1985).

- *Vaccinium vitis-idaea* (Ericaceae) is an evergreen erect dwarf-shrub that grows on exposed sites (wet and dry) with acid shallow, poorly developed mineral soils (Vander Kloet, 1988). This species has sexual and vegetative reproduction (Hall & Shay, 1981). It forms dense rhizomatous colonies. It is shade tolerant (Chapin & Shaver 1985).

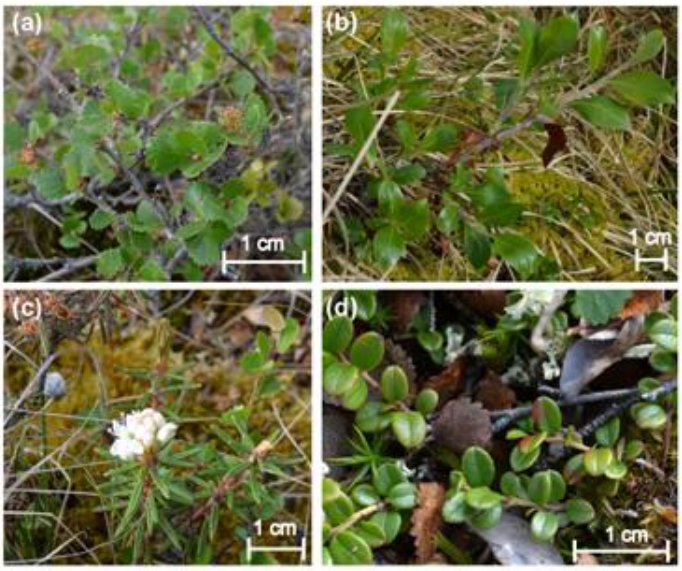

Figure 1.4: Study species: *Betula nana* (a), *Salix pulchra* (b), *Ledum palustre* (c), and *Vaccinium vitis-idaea* (d).

1.3 Aim and research questions

In my dissertation, I aim to explore the shifts in species diversity, community composition, and plant traits of tundra vegetation in a changing Arctic due to climate warming. These vegetation changes might feed back to regional climate through the surface energy budget and the water and carbon cycle (Foley *et al.* 2003; Chapin *et al.* 2005; Pearson *et al.* 2013). The importance of tundra vegetation–atmosphere–permafrost interactions in addition to the high vulnerability of this vegetation to climate change are the main motivation for this research.

Are species diversity and community composition related to edaphic factors in tundra ecosystems? If yes, do relationships differ according to plant functional types? (Chapter 2)

In high-latitude ecosystems, community assembly is mainly affected by edaphic factors and biotic interactions between vascular and nonvascular species (Cornelissen *et al.* 2001; Jägerbrand *et al.* 2006; Doxford *et al.* 2013). Several studies show a strong correlation between soil acidity or moisture and species diversity in tundra ecosystems (Gough *et al.* 2000; Chytrý *et al.* 2007). Although nonvascular species respond differently to environmental changes than vascular species, research has largely focused in the latter (Heikkinen & Neuvonen 1997; Gough *et al.* 2000; Sundqvist *et al.* 2011). The omission of nonvascular PFT in dynamic global vegetation models could result in inaccurate predictions of tundra ecosystem responses to climate change due to the higher abundance of nonvascular than vascular species in tundra and their important role in ecosystem functioning (Chapin & Shaver 1996; Matveyeva & Chernov 2000).

Do tundra shrubs grow faster in a warmer Arctic? (Chapter 3)

Shrub growth is suggested to be limited by air temperature and nutrient availability in arctic tundra ecosystems (Bliss 1962; Billings & Mooney 1968; Haag 1974; Chapin & Shaver 1996). Although studies using dendrochronological approaches show high correlation between shrub growth and air temperature (Blok *et al.* 2011a; Tape *et al.* 2012; Buchwal *et al.* 2013; Hollesen *et al.* 2015), this correlation could be driven by indirect temperature effects (e.g. increasing organic matter mineralization and thus nutrient availability), which are suggested to be more important that direct effects on experimental studies (Chapin *et al.* 1995; Hobbie & Chapin 1998; DeMarco *et al.* 2014). Faster shrub growth resulting in higher and denser shrub canopies with climate warming may lead to arctic shrub expansion by outcompeting other species for light and nutrients (Cornelissen *et al.* 2001; Sedia & Ehrenfeld 2003; Hudson, Henry & Cornwell 2011). Shrub expansion may affect important processes such as permafrost thawing, surface

albedo, carbon sequestration and litter production (Thompson *et al.* 2004; Beringer *et al.* 2005b; Chapin *et al.* 2005; Weintraub & Schimel 2005). Therefore, a better understanding of the mechanisms driving arctic shrub expansion is a first step in order to improve the accuracy of shift predictions of tundra vegetation and, thus, ecosystem functioning in a changing climate. Despite increasing efforts, uncertainties related to shrub growth sensitivity to climate remains (Elmendorf *et al.* 2012; Myers-Smith *et al.* 2015a).

Do shrub traits respond in a coordinated way to climate warming? (Chapter 4)
Plant traits are determined to a large extent by different trade-offs (Grime *et al.* 1997; Westoby *et al.* 2002). For example, the trade-off between the benefit of capturing light in shaded habitats and the cost of losing water by leaf transpiration determines leaf size of the plants (Parkhurst & Loucks 1972). Plants may change the allocation of resources to different functions (e.g. growth, reproduction) as a consequence of the variation of environmental conditions associated to climate warming, affecting therefore plant traits (Chapin *et al.* 1993). In case of tundra shrubs, several experimental studies have focused on changes in growth, mainly height and aboveground production (Chapin *et al.* 1995; Chapin & Shaver 1996; DeMarco *et al.* 2014). Shrub trait responses to increased air temperature and nutrient availability have been considered to a lesser extent and mostly accounting for individual trait responses (Hudson *et al.* 2011). Considering coordinated trait responses might provide a different picture of climate warming effects on shrub species. Moreover, taking into account coordinated trait responses will contribute to more realistic dynamic global vegetation models and robust predictions of shifts in vegetation, climate–vegetation feedbacks, and ecosystem processes (Sakschewski *et al.* 2015).

1.4 Thesis outline

To address the research questions, I used a combination of observational, experimental, and dendroecological approaches. In **Chapter 2** (published in Ecology and Evolution), I assessed the relationship of species diversity and community composition with soil variables on a set of observational plots that I established in two contrasting habitats in northeastern Siberian. In **Chapter 3**, I examined the effects of experimental soil warming and enhanced nutrient availability on the radial and vertical growth and stem traits of four tundra shrub species. I measured shrub growth ring widths to estimate growth rate, in addition to height and stem traits in individuals randomly selected from the experimental plots. In **Chapter 4**, I analysed the

effects of soil warming and increased nutrient availability on plant trait sets, growth strategy, and resource acquisition trade-off of four tundra shrubs. I measured seventeen plant traits related to growth, biomass, structure, and the leaf economics spectrum on individuals sampled from experimental soil warming and fertilization plots in a Siberian tundra ecosystem. I synthesized and discussed the main findings of these three chapters and future research in **Chapter 5**. Four appendices including metadata of the observational plots (**Appendix 1**), species composition list and abundance (**Appendix 2**), local flora of the research area (**Appendix 3**), and experimental soil temperature profile (**Appendix 4**) can be found at the end of this thesis.

1.5 References

See thesis section ‘References’.

CHAPTER 2

Interactive effects between plant functional types and soil factors on tundra species diversity and community composition

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"A few observation and much reasoning lead to error;
many observations and a little reasoning to truth"
(Alexis Carrel)

Interactive effects between plant functional types and soil factors on tundra species diversity and community composition

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Keywords: Active layer thickness – Carbon to nitrogen ratio – Cellulose to lignin ratio – Edaphic factors – Soil moisture – Nonvascular species – Soil pH – Vascular species – Vegetation cover.

Abstract

Plant communities are coupled with abiotic factors as species diversity and community composition both respond to and influence climate and soil characteristics. Interactions between vegetation and abiotic factors depend on plant functional types (PFT) as different growth forms will have differential responses to and effects on site characteristics. However, despite the importance of different PFT for community assembly and ecosystem functioning, research has mainly focused on vascular plants. Here, we established a set of observational plots in two contrasting habitats in northeastern Siberia in order to assess the relationship between species diversity and community composition with soil variables, as well as the relationship between vegetation cover and species diversity for two PFT (nonvascular and vascular). We found that nonvascular species diversity decreased with soil acidity and moisture and, to a lesser extent, with soil temperature and active layer thickness. In contrast, no such correlation was found for vascular species diversity. Differences in community composition were found mainly along soil acidity and moisture gradients. However, the proportion of variation in composition explained by the measured soil variables was much lower for nonvascular than for vascular species when considering the PFT separately. We also found different relationships between vegetation cover and species diversity according the PFT and habitat. In support of niche differentiation theory, species diversity and community composition were related to edaphic factors. The distinct

relationships found for nonvascular and vascular species suggest the importance of considering multiple PFT when assessing species diversity and composition and their interaction with edaphic factors. Therefore, identifying vegetation responses to edaphic factors is a first step towards a better understanding of vegetation–soil feedbacks under climate change. Our results suggest that incorporating differential responses of PFT is important for predicting vegetation shifts, primary productivity and in turn ecosystem functioning in a changing climate.

2.1 Introduction

Niche theory predicts that vegetation communities are coupled with abiotic factors because species both respond to and influence local climate and soil characteristics (Wookey *et al.* 2009; Medinski *et al.* 2010; van der Putten *et al.* 2013; Valladares *et al.* 2015). Changes in vegetation communities might thus affect climate through vegetation-radiation and vegetation–soil feedbacks among others (Chapin *et al.* 2000; Beringer *et al.* 2005). These interactions may be especially important in high latitude ecosystems which are expected to undergo large shifts in vegetation distribution as climate changes (Jägerbrand *et al.* 2006). Harsh environmental conditions, poorly developed soils and active cryogenic processes characterise high latitude ecosystems, providing a mosaic of vegetation communities across the landscape (Billings & Mooney 1968; Chernov & Matveyeva 1997; Walker 2000). In these ecosystems, community assembly is mainly affected by edaphic factors and biotic interactions between vascular and nonvascular species (Cornelissen *et al.* 2001; Jägerbrand *et al.* 2006; Gornall *et al.* 2011; Doxford *et al.* 2013). However, research has largely ignored the role of plant functional types (PFT) others than vascular plants, despite the differential processes interacting with PFT to promote community assembly and ecosystem functioning (Madrigal-González *et al.* 2012).

PFT are groupings of species which respond similarly to environmental conditions and affect ecosystem processes in similar ways (Lavorel *et al.* 1997). PFT have been broadly used in climatic models which predict vegetation shifts (Walker 2000). However, PFT classification and its level of detail depend on the spatial scale and the ecosystems and ecological processes under research. In arctic research, tundra vegetation is divided, in a first step, into vascular and nonvascular PFT (Chapin *et al.* 1996; Walker 2000). The vascular PFT includes shrubs and herbaceous (graminoids and forbs), while the nonvascular PFT comprises bryophytes and lichens (cryptogams). Both functional types are expected to change their distribution under

future climatic conditions (Cornelissen *et al.* 2001; Myers-Smith *et al.* 2011). Although the nonvascular functional type may respond differently to the environmental changes, frequently only several levels of vascular functional types are used in global vegetation models. The omission of nonvascular PFT could result in inaccurate predictions of tundra ecosystem responses to climate change due to the higher abundance of nonvascular than vascular species in high-latitude ecosystems and their strongly different responses to environmental factors (Tenhunen et al. 1992; Chapin & Shaver 1996; Matveyeva & Chernov 2000).

Community assembly is driven by biotic interactions, but also depends on environmental conditions (Cornwell & Ackerly 2009). Soil characteristics are strong predictors of species diversity and composition, especially in heterogeneous environments where the spatial distribution of vegetation species depends on their niche preferences (Björk *et al.* 2007; Sundqvist *et al.* 2011; Valladares *et al.* 2015). For example, studies show a strong correlation between soil acidity or moisture and species diversity (Gough *et al.* 2000; Chytrý *et al.* 2007). Diversity and distribution of species are also associated with patterns of mineral nitrogen and phosphorus availability in the soil, which is particularly important in ecosystems with low soil nutrient availability such as tundra (Gough & Hobbie 2003; Arnesen *et al.* 2007; Wardle *et al.* 2013). Climate change may have important effects on soil characteristics through increased soil temperature, fluctuations in moisture and enhanced nutrients (Keller *et al.* 2004; Seneviratne *et al.* 2010; IPCC 2013). As a consequence, species composition and diversity may change, likely affecting important ecosystem functions such as primary productivity (Hector *et al.* 1999; Balvanera *et al.* 2006; Cardinale *et al.* 2011).

Arctic tundra vegetation is adapted to harsh environmental conditions, such as extremely low temperatures, precipitation and soil nutrient availability (Billings & Mooney 1968). The vegetation grows slowly due to short growing seasons (less than three months) and is covered by snow for the rest of the year. The dependence of vegetation on edaphic factors, combined with small-scale heterogeneity in soil characteristics, promotes the patchy distribution of communities in tundra (Walker 2000; Lantz *et al.* 2010; Mod *et al.* 2014). Furthermore, nonvascular species can change the diversity and composition of vascular plant communities in tundra due to their strong effects on soil characteristics and on germination and establishment of seedlings (Sedia & Ehrenfeld 2003; Gornall *et al.* 2011; Doxford *et al.* 2013). Despite the importance of cryptogams, most studies on the relation between edaphic factors and species diversity and community composition have focused on vascular plants (Heikkinen & Neuvonen 1997; Gough

et al. 2000; Sundqvist *et al.* 2011; see exceptions: Jägerbrand *et al.* 2006; Löbel *et al.* 2006; Lang *et al.* 2012).

In the present study, we investigated the relation between vegetation and soil variables in a tundra ecosystem in northeastern Siberia in order to better understand the interactions between species diversity, community composition and soil variables, as well as the underlying edaphic factors promoting niche differentiation. We hypothesized that (i) species diversity and community composition of nonvascular and vascular PFTs are related to soil variables; (ii) vegetation cover correlates positively with species diversity; and (iii) the relationships among species diversity, community composition, vegetation cover and soil variables are PFT-specific. To test our hypotheses, we assessed the vegetation species diversity, community composition, cover, and several soil variables at two locations differing in topography and soil characteristics: a Pleistocene river terrace and a drained thaw lake basin. Due to their importance for tundra ecosystem functioning and vegetation–climate feedbacks, nonvascular species were considered in this study.

2.2 Materials and Methods

2.2.1 Study area and sampling design

The study area is located in the Kytalyk nature reserve in the Yana-Indigirka lowlands, Yakutia, northeastern Siberia (70°49'N, 147°28'E, 10 m.a.s.l.), in the continuous permafrost arctic region (Fig. 2.1). The mean annual air temperature is -13.1°C with minimum and maximum monthly means of -33.5°C in January and 11.3°C in July and the mean annual precipitation is 210 mm (1981–2013, WMO station 21946, Chokurdakh), mainly occurring during the growing season (about mid-June to end-August). Although 2013 was a slightly cold and dry year, both years of the study (2013 and 2014) had similar climates to the long-term averages.

Three geomorphological units are present at the study area: a Pleistocene yedoma hill, an alas – hereinafter referred to as ridge and lakebed – and a flood plain (Blok *et al.* 2010). Two cryogenic relief-forms are typical on the lakebed: low- and high-centred polygonal complexes. In the high-centred polygonal complex, wet hollows alternate with elevated polygons, which are higher and better drained.

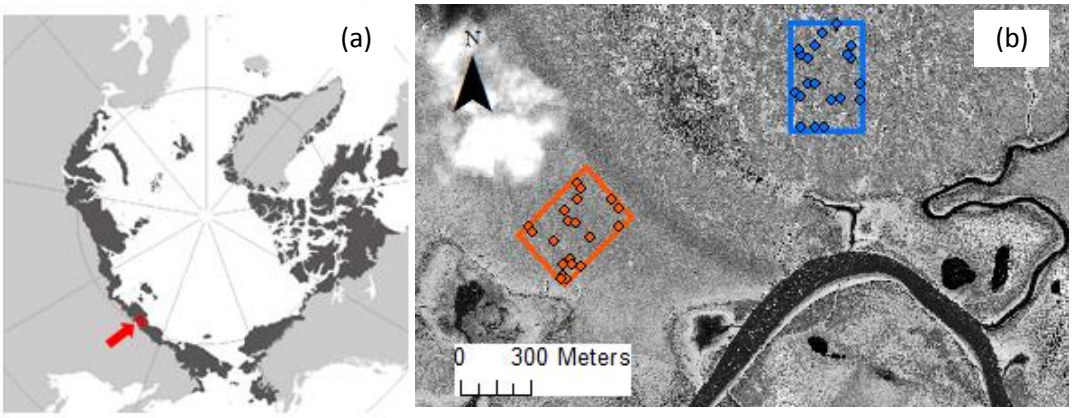

Figure 2.1: (a) Location of the study area (red point). In dark grey, extent of arctic tundra (data from Walker *et al.* (2005)); (b) Spatial distribution of the 40 plots selected to assess the species diversity: 20 plots placed on the lakebed (blue) and 20 plots on the ridge (orange). The background of the figure is a GeoEye-1 satellite image from August 2010.

The main vegetation present in the area is tussock-sedge tundra with abundant dwarf-shrubs on the ridge and, on the lakebed, sedge wetlands in the hollows and dwarf birch-moss communities on the polygons. High willow copses are characteristic for the flood plain. The tussock-sedge tundra is formed by low vegetation (3–25 cm) and comprises sedges (mainly *Eriophorum vaginatum*), deciduous (*Betula nana*, *Salix pulchra* and *Vaccinium uliginosum*) and evergreen dwarf shrubs (*Cassiope tetragona*, *Dryas octopetala*, *Ledum palustre* and *Vaccinium vitis-idaea*), mosses (mainly *Aulacomnium* spp., *Dicranum* spp., *Hylocomnium splendes* and *Tomentypnum nitens*) and lichens (mainly *Cetraria islandica, Flavocetraria cucculata* and *Peltigera* spp.). The sedge wetland (20–40 cm height) is dominated by *Eriophorum angustifolium* and peat mosses (*Sphagnum* spp.). The dwarf birch-moss communities are commonly dominated by *B. nana* (15–30 cm height) and various mosses (*Dicranum* spp., *Polytrichum* spp. and *Aulacomnium* spp.) with rather abundant grasses (*Calamagrostis holmii* and *Arctagrostis latifolia*) and lichens (*C. islandica* and *F. cucculata*). In the transition areas between hollows and polygons, the vegetation is 3–25 cm heigh. When the transitional area is closer to hollows, the vegetation is dominated by *Sphagnum* spp. with sparser cover of *E. angustifolium* and deciduous dwarf-shrubs (*B. nana, S. pulchra* and *Salix fuscenses*), while the vegetation is made up of evergreen dwarf-shrubs (*V. vitis-idaea*), mosses and abundant lichens (mainly *F. cucculata*) with spare cover of *B. nana* when the area is closer to polygons (see Appendix 2 for species name authority and complete species list).

We selected two contrasting habitats for the sampling: lakebed and ridge, to ensure that the main vegetation types present in the study area were included. We established 40 observational plots of 0.50 x 0.50 m in an area of 300 x 400 m on the ridge and lakebed (20 plots each). Thirty plots were established at the beginning of the 2013 growing season at random locations and, to improve replication for some of the communities, 10 additional plots were added at the beginning of the growing season of 2014 (Fig. 2.1).

2.2.2 Species diversity, community composition and vegetation cover

In order to assess the species diversity and community composition, we used a plot-size grid divided in 25 quadrats of 0.10 × 0.10 m. We placed the grid on each of the 40 selected plots and identified all the species, including cryptogams, within each quadrat. The diversity surveys were carried out during the mid-growing season in 2013 (6-10th July on the plots selected in 2013) and 2014 (7-8th July on the plots selected in 2014). Vegetation samples were collected when field identification was difficult, which was the case for practically all bryophytes and lichens, and sent to the Komarov Botanical Institute (Russian Academy of Sciences) for identification. We further assigned each species to one of the two following plant functional types (PFT): vascular (shrubs and herbaceous) and nonvascular (bryophytes and lichens) (*sensu* Walker 2000). We described the diversity for every plot and PFT using the species richness (number of species of each PFT present in a plot) and Shannon-Wiener diversity index (Shannon 1948). The community composition was defined as the list of species on each plot including their abundance (estimated as number of grid quadrats where a species was present).

We estimated vegetation cover using a modified point-quadrat method (Jonasson 1988). We placed the grid described above on each of the 30 plots selected in 2013 and passed a metal rod (2 mm diameter) vertically down at every quadrat intersection. We registered all the contacts with the vegetation, including woody parts and standing litter, from the top layer to the moss layer bottom. The cover was determined adding the number of hits for all the species belonging to each PFT on every plot. The cover surveys were carried out during the mid-growing season in 2013 (20-30th July).

2.2.3 In situ measurements of soil variables

We measured soil temperature (ama-digit ad15th digital thermometer, Amarell GmbH & Co., Germany), soil acidity (DM-13 pH-meter, Takemura Electric Works, Ltd., Japan) and soil moisture (Theta Probe ML1, Delta T Devices Ltd., UK) in five quadrats of the grid used for the diversity assessment at 10 cm depth in every plot. We also measured active layer thickness as the distance between permafrost and soil surface, including the moss layer if present. For that, we introduced a metal rod with centimetre scale vertically into the soil to the depth of resistance at the sampling locations where the other soil variables were measured. For every soil variable and plot, the five quadrat measurements were averaged. We measured the soil variables in mid-July 2014 in all 40 plots. Due to the slow turnover in species composition of tundra communities, we assume that between plot differences are more important in explaining species diversity and composition compared to variability between two consecutive years.

2.2.4 Soil sampling and analysis

We sampled two soil cores per plot (4.8 cm diameter × 5.3 cm height) in mid-July 2013 (30 plots) and 2014 (10 plots added this year). We determined bulk density by air-drying the soil samples for three weeks. Once in the laboratory, the samples were oven-dried at 70°C for 48 hours, ground, sieved through a 2 mm mesh and milled. Carbon and nitrogen content were analysed in subsamples of about 2.5-3.0 mg using a TruSpec Micro CHN analyser (Leco Corporation, USA). Then, the ratio carbon to nitrogen was calculated. We determined the cellulose and lignin content in milled 10 mg subsamples by diffuse reflectance infra-red Fourier transform spectroscopy (Tensor 27, Bruker Optics GmbH, Fällanden, Switzerland). Spectra were acquired by averaging 64 scans per sample at 4 cm^{-1} resolution over the range 4000-400 cm^{-1}. Powdered KBr was used to create a reference background spectrum and chernozemic soils (Hildesheim-Braunschweig, Germany) as standard material for the calibration curve. We integrated the peaks corresponding to cellulose (1260-1210 cm^{-1}) and lignin (1510-1500 cm^{-1}) and calculated the ratio of cellulose to lignin. Every soil variable determined was averaged per plot.

2.2.5 Data analysis

We analysed species diversity as a function of site, PFT and their interaction with a linear mixed-effect model. The fixed terms were site (factor with two levels: ridge and lakebed) and

PFT (factor with two levels: vascular and nonvascular). Plot was fitted as random factor (40 levels).

In order to explore the relationships between species diversity and soil variables across the 40 plots, standardized soil data were subjected to a Principal Component Analysis (PCA) using the vegan package version 2.3-1 (Oksanen 2015) in R (http://r-project.org). Then, species diversity was analysed as a function of the interactions of site and PFT with the loadings of the two first PC axes (fixed terms) using a linear mixed-effect model. Plot was considered a random term (40 levels).

To test the relationship between community composition and soil variables, the species abundances were subjected to a Canonical Correspondence Analysis (CCA) using the vegan package. The species data were scaled to unit variance to account for differences in abundance distribution (rare species). We constrained the ordination using the standardized soil variables.

We used a linear mixed-effect model to test if vegetation cover was sparser in communities with lower species diversity than in more diverse communities. We analysed the cover and diversity data that were collected in 2013. We considered the interaction among species diversity (a continuous variable), PFT (two factors: vascular and nonvascular) and site (two factors: ridge and lakebed) a fixed term and plot as a random term (29 levels; to facilitate the analysis, one lakebed plot corresponding to a community without nonvascular species was eliminated). Vegetation cover was expressed as number of hits per grid quadrat. Two extreme values of the vascular cover on the ridge were detected based on model residual values that were more than three times and a half the median absolute deviation (pascal package). The extreme values were removed prior to analysing the relation between cover and Shannon-Wiener index.

We performed the statistical analysis using R 3.2.2. The linear mixed-effect models we used to test our hypotheses were fitted in asreml (ASReml 3.0, VSN International Ltd., UK).

2.3 Results

2.3.1 Species diversity

Twenty-five vascular and 53 nonvascular species (29 lichen and 24 bryophyte species) were identified in the 40 plots. Species richness ranged from 1 to 30 species per plot with a mean of 15 species (60% of them were nonvascular).

Nonvascular diversity (Fig. 2.2) was significantly higher than vascular diversity in both sites (richness $F_{1,39}$ = 32.8, P < 0.001; Shannon-Wiener index $F_{1,39}$ = 28.0, P < 0.001). Species diversity was also significantly higher on the ridge than on the lakebed (richness $F_{1,39}$ = 21.1, P < 0.001; Shannon-Wiener index $F_{1,39}$ = 8.41, P < 0.01).

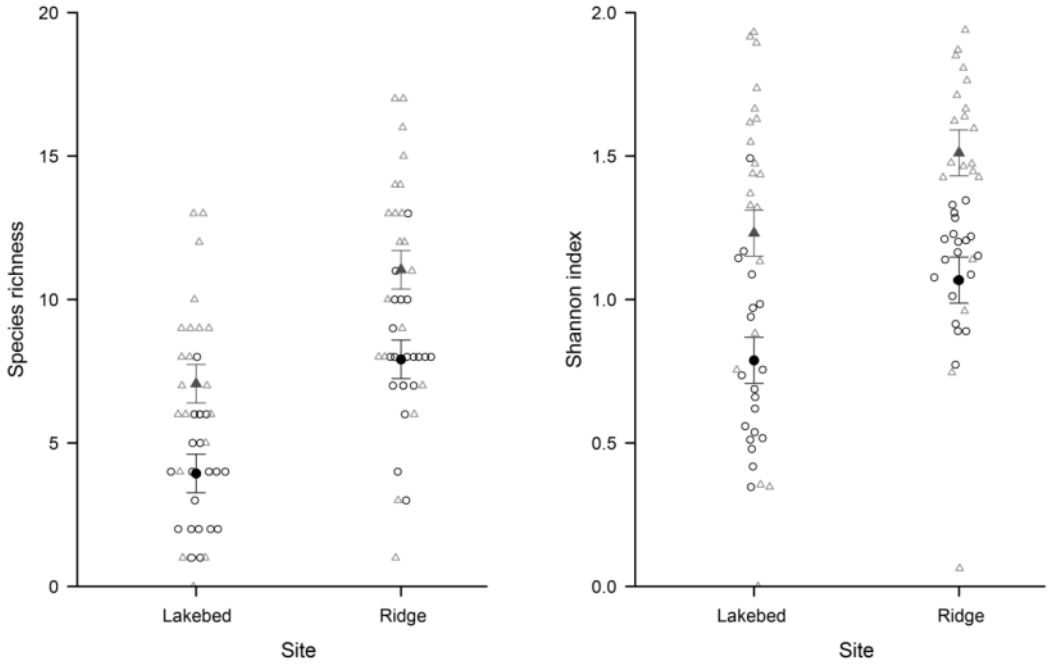

Figure 2.2: Species richness (left) and Shannon index (right) on lakebed and ridge for nonvascular (open circles) and vascular (open triangles) plant functional types of the 40 selected plots. Close circles and triangles represent the mean diversity predicted by the model for both PFT. Error bars are the standard error of the predicted values.

2.3.2 Soil variables

Overall the soil was acidic (pH < 6.5), rich in organic matter with a low bulk density (mean ± standard deviation: 0.455 ± 0.263 g/cm^3). Soil organic matter had not decomposed extensively as the cellulose to lignin and carbon to nitrogen ratios indicated (1.83 ± 1.00 and 21.7 ± 4.0). The measured soil variables were highly variable among plots and differed between lakebed and ridge, except for soil moisture and carbon to nitrogen ratio. On average, bulk density, pH and cellulose to lignin ratio were lower for soils on the lakebed than on the ridge (Table 2.1). The active layer was also thinner for lakebed soils, while temperature, carbon and nitrogen contents were higher than for ridge soils. The quality of soil organic matter was comparable between both sites (no differences in the carbon to nitrogen ratio), although the decomposition rate may have been higher on the lakebed (lower cellulose to lignin ratio).

When analysed with a PCA, soil data were separated into lakebed and ridge plots (site) by the first PC axis (Fig. 2.3). The first PC axis was mainly related to nitrogen and carbon content, cellulose to lignin ratio and dry bulk density, explaining 43% of the variation among plots. The second PC axis explained 24% of the total variation in soil data and was related to moisture, pH and active layer thickness (ALT).

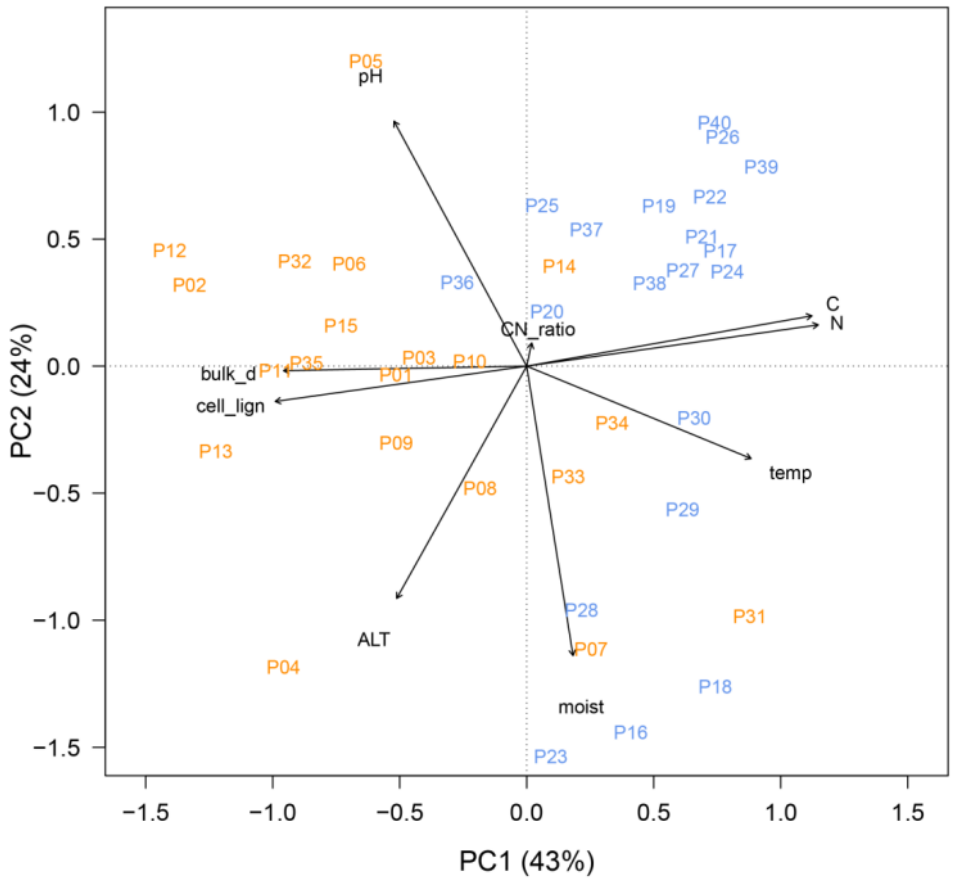

Figure 2.3: Principal component biplot of the soil variables measured across the 20 plots selected on the ridge (in orange) and the 20 plots selected on the lakebed (in blue). The soil variables include pH, moisture (moist), temperature (temp), active layer thickness (ALT), dry bulk density (bulk_d), carbon content (C), nitrogen content (N), carbon to nitrogen ratio (CN_ratio) and cellulose to lignin ratio (cell_lign). The first component explains 43% of the total variance, while the second component explains the 24%.

Table 2.1: Summary of the soil variables measured on lakebed and ridge plots. Minimum (Min), maximum (Max), mean and standard deviation (SD) values are included.

	Lakebed				Ridge			
	Min	**Max**	**Mean**	**SD**	**Min**	**Max**	**Mean**	**SD**
Dry bulk density (g/cm^3)	0.128	0.530	0.310	0.090	0.297	1.20	0.601	0.299
Moisture (%)	17.8	70.2	35.9	19.1	15.3	69.7	38.2	15.3
pH	4.90	6.40	5.84	0.44	5.30	6.60	6.11	0.35
Active layer thickness (cm)	14.1	42.5	24.9	8.8	14.9	47.9	34.6	7.7
Temperature (°C)	3.90	7.90	6.44	1.04	2.50	9.20	4.77	1.40
Carbon content (%)	13.4	42.3	27.2	7.9	2.3	31.7	14.8	9.4
Nitrogen content (%)	0.69	1.95	1.28	0.33	0.13	1.62	0.68	0.44
Carbon to nitrogen ratio	18.1	35.1	21.4	4.8	18.0	32.5	22.0	3.2
Cellulose to lignin ratio	0.53	3.30	1.25	0.77	0.76	3.77	2.41	0.86

2.3.3 Species diversity–soil variable relations

To determine the relations between species diversity and soil variables, we used the loadings of the two first axes of the PCA. We found that species richness was related to the first PC axis, while Shannon-Wiener index was related to the second PC axis when analysing the interactive effects of soil variables and site (species richness $F_{1,39} = 8.16$, $P < 0.01$; Shannon-Wiener index $F_{1,39} = 7.27$, $P < 0.05$). These relationships were different between ridge and lakebed. Species richness decreased with increasing carbon and nitrogen content and decreasing cellulose to lignin ratio and bulk density on the ridge and remained unresponsive for those variables on the lakebed. The Shannon-Wiener index decreased with soil acidity, moisture, temperature and ALT on both ridge and lakebed, although the relationship was stronger on the lakebed compared to the ridge (Fig. 2.4).

Species diversity was related to the second PC axis when analysing the interactive effects of soil variables and plant functional type (PFT) (species richness $F_{1,39} = 12.5$, $P < 0.01$; Shannon-Wiener index $F_{1,39} = 21.8$, $P < 0.001$). This relationship was different for vascular and nonvascular diversity. Nonvascular diversity increased with decreasing soil acidity, moisture, temperature and ALT, while vascular plants were unresponsive to these variables (Fig. 2.4)

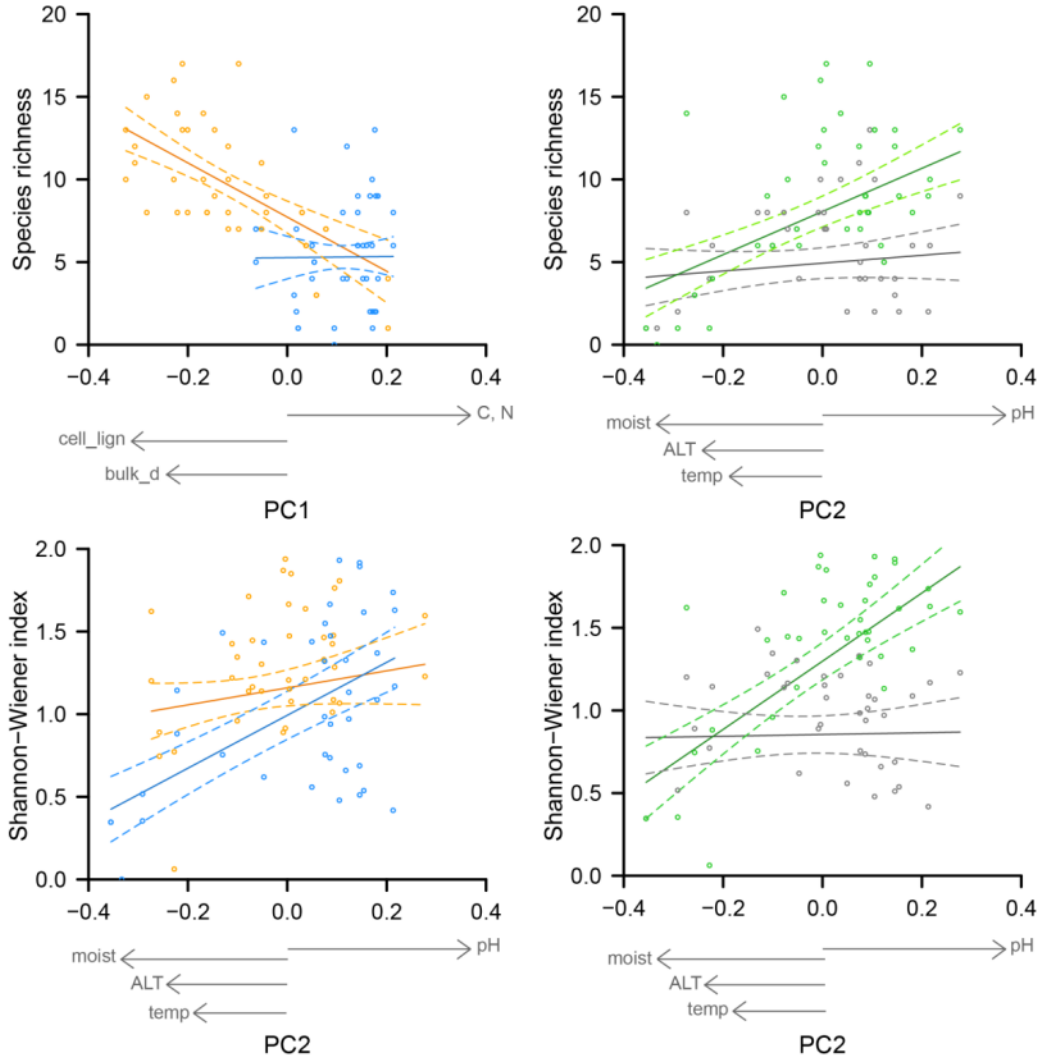

Figure 2.4: Species diversity relationships with the soil variables by site (lakebed (blue), ridge (orange)) and plant functional type (vascular (grey), nonvascular (green)). The top panels show the species richness and the bottom panels the Shannon-Wiener index relationships. Solid lines are the values predicted by the linear mixed-effect model, dashed lines are the upper and lower limits of the confidence interval of the predicted values and points are measured data. The main soil variables comprising the first and second principal component axes (grey arrows) are carbon content (C), nitrogen content (N), cellulose to lignin ratio (cell_lign), dry bulk density (bulk), pH, moisture (moist), active layer thickness (ALT) and temperature (temp).

2.3.4 Community composition–soil variable relations

To explore the relationship between community composition and soil variables, the species abundance was subjected to a Canonical Correspondence Analysis (CCA) constrained by the soil variables. The analysis showed that 37% of the total variance of the community composition was explained by the soil variables when including both PFTs together. Species were arranged mainly along the gradients of soil acidity and moisture in this case. The explained proportion of variance of the vascular composition (42%) was higher compared to the nonvascular composition (28%) when considering each PFT alone. Vascular composition was mainly related to the gradients of soil acidity, temperature, moisture and nitrogen content (principal components of the first CC axis that explained 48% of the response variance) (Fig. 2.5). Nonvascular composition was related to soil moisture and acidity gradients (main components of the first CC axis explaining 27% of the response variance) and, to a lesser extent, gradients of nitrogen content, cellulose to lignin and carbon to nitrogen ratios, soil temperature and ALT (principal components of the second CC axis explaining 23% of the response variance) (Fig. 2.5).

2.3.5 Vegetation cover–species diversity relations

We found that vegetation cover was related to species diversity (species richness $F_{1,28} = 19.3$, $P < 0.001$; Shannon-Wiener index $F_{1,26} = 48.5$, $P < 0.001$). This relationship was different for site and PFT (Fig. 2.6). Vascular cover was positively related to species diversity on the lakebed. However, the relationship was negative on the ridge. The nonvascular cover increased slightly with species diversity on the lakebed. On the ridge, nonvascular cover increased with the Shannon-Wiener index, but remained constant with the species richness.

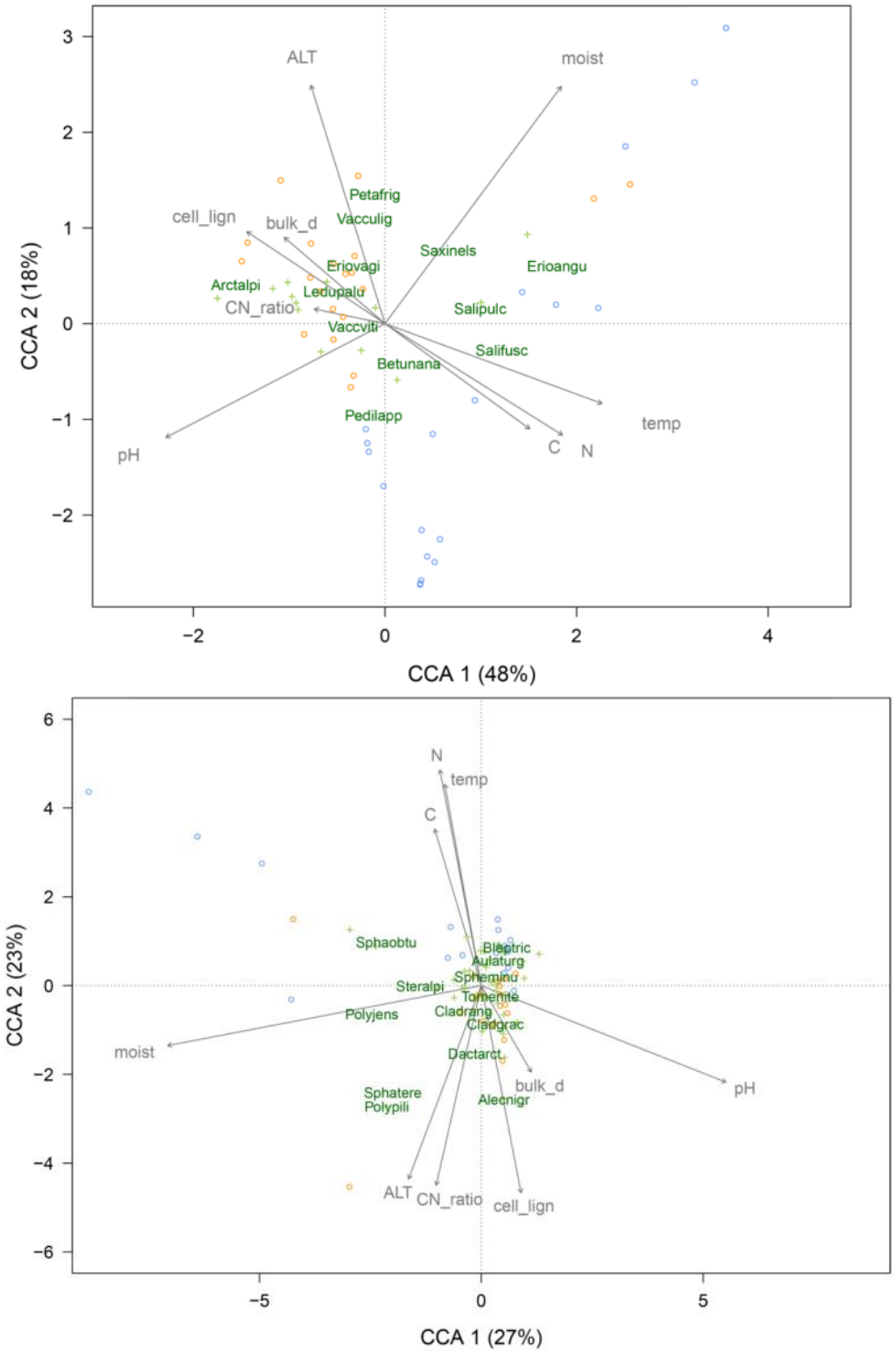

Figure 2.5: Canonical correspondence analysis (CCA) ordination diagrams of the community compositions for both plant functional types (PFT): vascular (top) and nonvascular (bottom) on the selected plots constrained by soil variables. The first component explains 48% of the total variance for vascular and 27% for nonvascular PFTs, while the second component explains 18% and 23% respectively. Dominant species (green text), the rest of species (green cross), lakebed plots (blue circles), ridge plots (orange circles) and soil variables (arrows) are shown. See tables in Appendix 2 for complete name of the species. The soil variables include pH, moisture (moist), temperature (temp), active layer thickness (ALT), dry bulk density (bulk_d), carbon content (C), nitrogen content (N), carbon to nitrogen ratio (CN_ratio) and cellulose to lignin ratio (cell_lign).

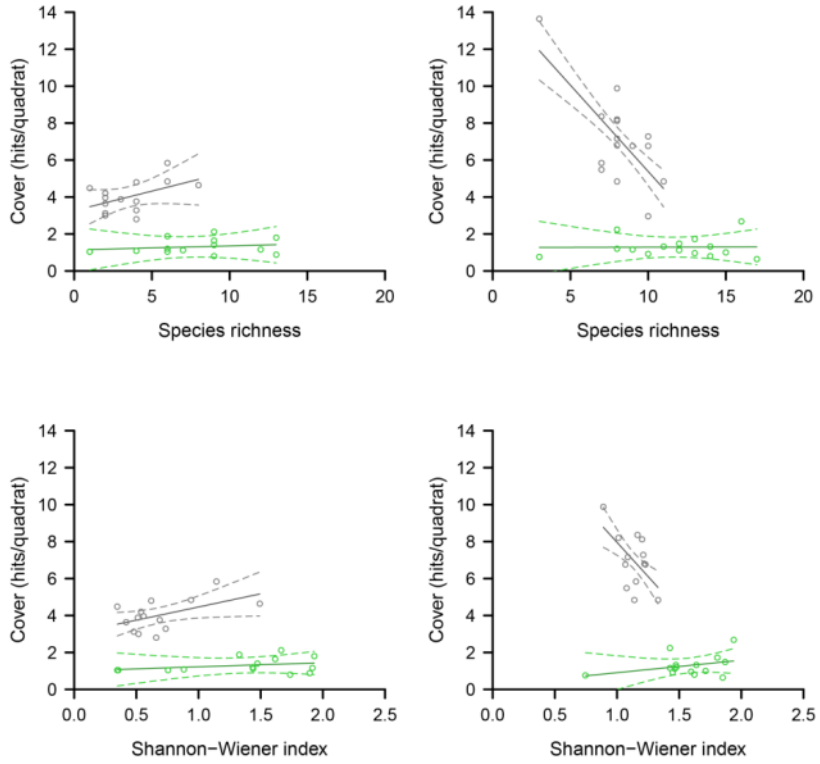

Figure 2.6: Relationship of the vegetation cover with the diversity. The vegetation cover is expressed as the total number of hits per grid quadrat in each plot for vascular (grey) and nonvascular (green) species. The left panels show the relations found on the lakebed and the right panels on the ridge. Points represent the cover measured in the plots. Solid lines are the predictions of the model and dash lines the confidence interval of the predictions.

2.4. Discussion

We explored the relationships among species diversity, community composition and soil variables and between vegetation cover and species diversity accounting for nonvascular and vascular plants in an arctic tundra ecosystem. Our findings show, as we hypothesised, that the relationships were PFT-specific. Nonvascular diversity was related to soil variables (negatively related to acidity, moisture, temperature and ALT), but, surprisingly, vascular diversity was unrelated to soil variables when considering multiple variables simultaneously. Community composition was also related to soil variables, finding important differences in composition along soil acidity and moisture gradients. However, the proportion of variation in composition explained by soil variables was much lower for nonvascular than for vascular species. Because these results show differential responses of PFT to edaphic factors, they confirm the importance of taking into account multiple PFT when studying interactions among species diversity and composition, edaphic factors and ecosystem functioning, especially in these harsh arctic ecosystems.

2.4.1 Species diversity

We found low species diversity with higher nonvascular than vascular diversity in the observational plots, which is characteristic of high latitude ecosystems (Billings & Mooney 1968; Gough *et al.* 2000; Sitch *et al.* 2007). In these ecosystems, bryophytes and lichens form a predominant PFT that contributes to species diversity due to the fact that cryptogams are often better adapted to harsh environmental conditions than vascular plants (Callaghan *et al.* 2005; Jägerbrand *et al.* 2006; Lang *et al.* 2012; Virtanen *et al.* 2013).

We also found higher species diversity on the ridge than on the lakebed. Similar to other arctic areas, the ridge is more wind- and runoff-exposed than the lakebed, resulting in a thinner snow layer on the ridge (Wahren *et al.* 2005; Bruun *et al.* 2006). As the maximum canopy height in arctic tundra is conditioned by the thickness of the winter snow layer, communities on the ridge are shorter than on the lakebed (Bilbrough *et al.* 2000; Essery & Pomeroy 2004). The exclusion of dominant species as a consequence of the exposure, together with less cover shading and leaf litter deposition, may explain the higher species diversity of the ridge communities, especially the greater number of nonvascular species. Furthermore, nanorelief forms on the ridge resulting from cryogenic processes (tussocks) can provide shelter to several species. In contrast with the ridge, the communities on the lakebed are dominated in abundance and cover by one or two vascular species. On these communities, dominant species prevent other species from establishing and competitively exclude nonvascular vegetation (strong light competition through vascular cover shading and leaf litter deposition), declining the species diversity (Cornelissen *et al.* 2001; Sedia & Ehrenfeld 2003; van der Wal *et al.* 2005; Startsev *et al.* 2008; Odland *et al.* 2015).

2.4.2 Soil variables

Similar to other tundra ecosystems, the soil in our study area was acidic and rich in organic matter (Walker 2000). Low temperature and water logging, together with the litter quality and functional composition (e.g. high abundance of evergreen dwarf-shrubs) may limit the decomposition of the soil organic matter (Oades 1988; Aerts 2006). The characteristic soil heterogeneity of high latitude ecosystems was reflected by the high variation of the soil variables among plots (Billings & Mooney 1968).

Differences found between soil variables on lakebed and ridge might be associated with the vegetation type present in each location. For example, the lower bulk density and soil pH on the

lakebed than on the ridge might be related, respectively, to high litter deposition in dwarf birch-moss communities and to methanogenic processes linked to the anaerobic conditions of sedge wetland soils (Rawls 1983; Christensen *et al.*1995; Inglett *et al.* 2005).

2.4.3 Species diversity–soil variable relations

We hypothesised that species diversity and edaphic factors were related as reported in several studies (Ma 2005; Löbel *et al.* 2006; Gargano *et al.* 2010; Lai *et al.* 2015). We found that nonvascular diversity was negatively related to soil acidity, moisture, soil temperature and ALT when considering several soil variables simultaneously. This relationship confirms our hypothesis for cryptogams and is in line with previous findings showing effects of soil variables on species diversity, which in turn can locally modify the soil characteristics (Loreau *et al.* 2001; Sedia & Ehrenfeld 2003; Gornall *et al.* 2011). However, vascular diversity was unrelated to edaphic factors, contrary to what we expected. Although the species composition may vary among locations due to different species physiological tolerance to soil variables (Billings & Mooney 1968; Theodose & William 1997; Eskelinen *et al.* 2009), the diversity may remain constant (i.e. different species but same number and abundance), which would overshadow any response. Furthermore, opposite trends in response to individual soil variables (e.g. increase of diversity with pH or decrease with moisture or ALT) might be hidden when considering multiple soil variables at the same time and therefore mask specific relationships.

2.4.4 Community composition–soil variable relations

Less than half the variance of the community composition was explained by edaphic factors, suggesting that the rest may be explained, in part, by biotic factors, such as competition (e.g. light shading of nonvascular vegetation by vascular plants) and facilitation (e.g. vascular seedling recruitments and frost protection by nonvascular species) (Sedia & Ehrenfeld 2003; Gornall *et al.* 2011; Virtanen *et al.* 2013; Odland *et al.* 2015). The presence of a root system and its differences among species might explain the stronger relationship between community composition and edaphic factors for vascular than for nonvascular species.

Nonvascular and vascular PFT comprise species differing in their functional traits (e.g. phenology or rooting system) and, thus, in their niche preferences (Valladares *et al.* 2015). This niche partitioning might explain our results showing variation in community composition along different soil gradients when accounting for PFT. Vascular community composition was mainly related to soil acidity, temperature, moisture and nitrogen content. These soil variables can

modify the nutrient and water availability, which discriminate among vascular species according to their root characteristics (McKane *et al.* 2002). Nonvascular composition was related to soil moisture, acidity, temperature, ALT, nitrogen content and cellulose to lignin and carbon to nitrogen ratios. Soil moisture and factors related to soil organic matter (cellulose to lignin and carbon to nitrogen ratios) and nutrient availability might discriminate between lichens and bryophytes, as lichens grow in drier and N-poorer soils (Sedia & Ehrenfeld 2003; Cornelissen *et al.* 2007; Virtanen *et al.* 2013). Soil moisture and acidity might also separate *Sphagnum* spp. from other bryophyte species by their different physiological tolerance (Weston *et al.* 2015). *Sphagnum* spp. are more abundant in wet acidic soils than other bryophyte species due to their higher tolerance to water stress and soil acidity (Gough *et al.* 2000; Elumeeva *et al.* 2011). The relationship between nonvascular composition and ALT might be associated with the thermal insulation properties of the bryophyte layer, which will depend on the species and its thickness (Walker *et al.* 2003; Gornall *et al.* 2007). ALT may also have indirect effects on nonvascular communities by benefiting vascular plants, which can reach nutrients that are available at greater soil depth with their root system and, thus, out-compete nonvascular species, which are limited to the surface, for mineral resources (Keuper *et al.* 2012; Wang *et al.* 2016).

2.4.5 Vegetation cover–species diversity relations

Vegetation cover and species diversity were related according to our results, although the relationship was different depending on site and PFT. On the lakebed, vascular cover increased with increasing species diversity. In communities where the two dominant species on the lakebed (*B. nana* and *E. angustifolium*) form sparser canopies, higher number of species can coexist because of reduced shading. The non-dominant species occupy different layers within the canopy, overlapping in many cases. These layers might explain the positive correlation between cover and diversity, as the point-quadrat method we used allows us to take the vertical canopy structure into account. However, on the ridge and contrary to our hypothesis, vascular cover was higher in less diverse communities. This negative correlation might be explained by two main factors. On one hand, communities with the lowest species diversity are found in sedge wet hollows, which are dominated generally by *E. angustifolium*. This species grows faster and produces more biomass than the other species, resulting in higher cover and litter deposition, which limit the number of coexisting species due to resource and light competition. Additionally, the depressions where those communities grow accumulate greater amounts of snow compared to other habitats, allowing higher individuals than in more diverse communities.

On the other hand, we might have underestimated the vascular cover of diverse communities on the ridge (as well as the nonvascular cover) due to the small size of the individuals comprising these communities in relation to the rather coarse grid cells of our sampling scheme.

Aboveground biomass has been widely used as a proxy of productivity (Chiarucci *et al.* 1999; Fraser *et al.* 2015). In tundra, aboveground biomass and production are highly correlated (Webber 1978). Furthermore, vegetation cover and aboveground biomass were correlated in different ecosystems (Grytnes 2000; Zhang *et al.* 2016). These correlations and our results for the lakebed suggest that primary productivity and species diversity are positively related, supporting previous findings, although not in the case of the ridge (Tilman *et al.* 1996; Loreau *et al.* 2001; Hooper *et al.* 2005). This relationship inconsistency between sites may be attributed to complex mechanisms controlling species diversity and productivity (Grace *et al.* 2016). Further efforts to improve the vegetation cover estimation and explore the actual relations among cover, biomass and productivity in the study area, will provide a better understanding of the species diversity role in ecosystem functioning in Siberian tundra.

2.4.6 Climate change and tundra vegetation

Air temperature and precipitation are projected to increase in the Arctic by around 3°C and 20% respectively (emission scenario RCP4.5, IPCC 2013). How these changes will propagate into edaphic factors, such as soil temperature, moisture or active layer thickness, remains uncertain in terms of direction and spatial variability (Walvoord & Kurylyk 2016). Our study highlights that tundra vegetation is closely related to a combination of edaphic factors going beyond soil acidity and moisture only. It is therefore important to increase our understanding of how atmospheric changes propagate into edaphic factors for more reliable predictions of vegetation shifts.

In addition to edaphic factors, several complex interactions and buffering mechanisms (e.g. competition and facilitation) will determine species diversity and community composition (Chapin & Shaver 1996). For example, under a scenario of increased soil temperature and moisture, mineralization rates of soil organic matter are expected to rise, resulting in a higher nutrient availability (Schmidt *et al.* 1999). In addition, the release of organic acids during the decomposition process will increase soil acidity (Satchel 1974). According to our results, nonvascular diversity may decrease due to these expected changes in edaphic factors, while vascular diversity may remain constant. Shifts in community composition may also be caused by direct (e.g. changes in soil conditions) or indirect effects. For instance, soil warming and higher

nutrient availability may increase the height and abundance of graminoids and shrubs, which will outcompete nonvascular species (Hudson *et al.* 2011). These vegetation shifts will result in feedbacks to energy fluxes, permafrost thawing and soil conditions, which may stabilize or accelerate those changes. In case of permafrost thawing, increasing soil temperature may promote a rise in active layer thickness (Ritcher-Menge & Overland 2010), but vegetation shifts, such as an expansion of shrub cover, may protect permafrost from thawing through soil shading (Blok *et al.* 2010; Nauta *et al.* 2014). On the other hand, an increasing decomposition rate may lead to a decrease of standing litter in wet sedge dominated areas, resulting in less soil shading (Juszak *et al.* 2016).

In summary, because of uncertainties in responses of edaphic factors to projected climatic conditions and complex feedbacks involved in vegetation shifts, species diversity and community composition predictions based only on changes of edaphic factors may be highly inaccurate. However, identifying the vegetation responses to edaphic factors is a first step for a better understanding of vegetation–soil feedbacks under climate change. The distinct relationships found for nonvascular and vascular species suggest the importance of considering multiple PFT for predicting vegetation shifts, primary productivity, and in turn ecosystem functioning in a changing climate.

2.5 Acknowledgements

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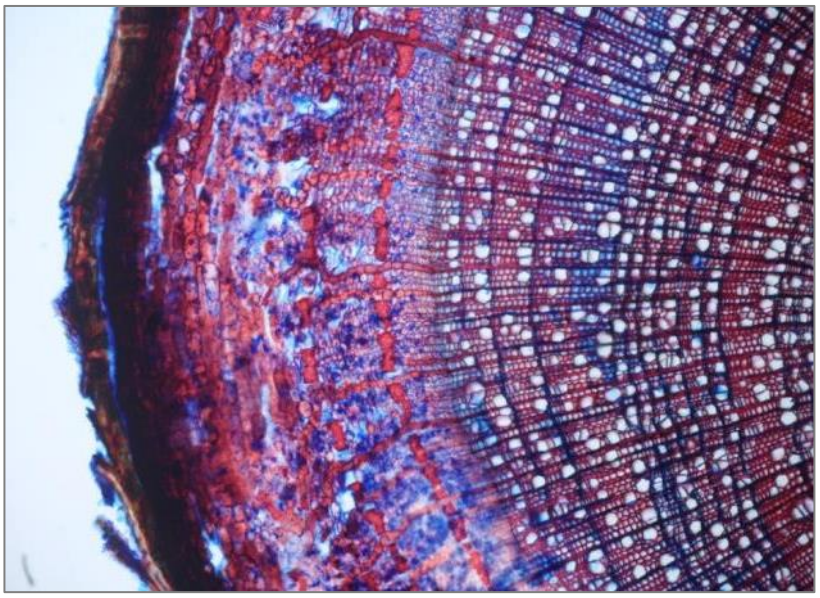
2.6 References

See thesis section 'References'.

CHAPTER 3

Shrub growth rate and bark responses to soil warming and nutrient addition – an experimental dendroecological approach



Shrub growth rate and bark responses to soil warming and nutrient addition – an experimental dendroecological approach

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Abstract

Tundra shrubs are slow-growing species limited by low air temperature and scarce nutrient availability. However, shrub expansion has been widely observed in the Arctic during the last decades and attributed to climate warming. Shrub expansion affects the surface albedo and permafrost thawing among others, which may feed back to climate. Despite the importance of tundra vegetation–climate feedbacks and research efforts done, uncertainties of shrub growth sensitivity to climate remain. Here, we explored the effects of climate warming on shrub growth (vertical and radial), bark thickness, and bark investment in four arctic shrub species. For that, we combined experimental manipulation of two suggested growth drivers – soil temperature and nutrient availability – with dendroecology in a Siberian tundra ecosystem. Shrub growth was mainly limited by nutrient availability and not by soil temperature, according to our results. We also found negative treatment combination effect on bark thickness and negative correlation between bark investment and growth rate for some of the species. Moreover, shrub response to treatment was species-specific. These findings suggest that tundra shrubs, especially deciduous species, will grow faster and taller driven by indirect effects of climate warming (i.e., enhanced nutrient availability). However, shrubs might become more vulnerable to pests, herbivory, and climate extremes, such as frost or drought events, due to thinner bark and lower bark investment. Experimental dendroecological approaches simulating projected climate scenarios for the Arctic, and an increasing number of study species and locations will reduce uncertainties related to

shrub growth sensitivity to climate, providing insight into shrub expansion–climate feedbacks in tundra.

3.1 Introduction

Global air temperature is unequivocally increasing, more rapidly in the Arctic – where air temperature is projected to rise by around 3°C (emission scenario RCP4.5) – than in other regions (IPCC 2013). As a consequence of this change, an increase in soil temperature is expected. Higher soil temperatures in the Arctic will have effects on tundra vegetation diversity, distribution, and plant traits by direct and indirect effects (van Wijk *et al.* 2003; DeMarco *et al.* 2014; Edwards & Henry 2016). Examples of indirect effects are permafrost thawing, which will release nutrients trapped in the permafrost (Schuur *et al.* 2009; Romanovsky, Smith & Christiansen 2010), and higher soil organic matter mineralization rates resulting in more nutrients available for vegetation (Schmidt, Jonasson & Michelsen 1999; Walther *et al.* 2002). Despite the importance of tundra vegetation–climate feedbacks and increasing efforts to understand species sensitivity to climate, the latter remains uncertain in terms of direction and spatial variability (Elmendorf *et al.* 2012; Myers-Smith *et al.* 2015a).

Tundra vegetation is adapted to harsh environmental conditions, such as extremely low temperatures, low precipitation, and scarce soil nutrient availability, and to a short growing season (< 3 months) (Billings & Mooney 1968; Crawford 2008). For that, tundra vegetation adopts a slow-growth strategy, with high persistence and efficient use of resources (Chapin 1980a; Reich, Walters & Ellsworth 1997; Cornelissen 1999). The low rate of tissue turnover allows these species to allocate resources to storage or defence structures (e.g., bark), conferring vegetation resistance to stress (Chapin, Autumn & Pugnaire 1993). Wood and bark provide essential functions to shrubs such as mechanical support of aboveground tissues, conduction of sap, storage of resources, and protection against herbivory, pathogens, and frost damage (Francis and Vavrus, 2012; Paine et al., 2010; Poorter et al., 2014; Vines, 1968). These functions may reduce the vulnerability of shrubs to climate extremes, which are projected to become more frequent (IPCC 2013). Despite the slow-growth strategy adopted by tundra vegetation, shrub expansion has been reported in many arctic, subarctic, and alpine regions using repeat aerial photography, satellite imagery, and long-term monitoring plots (Sturm, Racine & Tape 2001; Tape, Sturm & Racine 2006; Tape *et al.* 2012; Myers-Smith *et al.* 2011).

Shrub expansion can take place by lateral and vertical growth, recruitment between existing patches or colonization of new areas involving an increase in shrub cover or biomass (Myers-Smith *et al.* 2011). Arctic shrub expansion is spatially and temporally heterogeneous, which can partly be attributed to different shrub growth strategies and sensitivity to climate (Blok *et al.* 2010; Kremers, Hollister & Oberbauer 2015; Myers-Smith *et al.* 2015a). Although summer air temperature is considered to be the main driver of shrub expansion (Forbes, Fauria & Zetterberg 2010; Hallinger, Manthey & Wilmking 2010; Blok *et al.* 2011a), other mechanisms have been proposed as controlling environmental factors, such as summer precipitation, active layer thickness, and soil nutrient availability (Sturm *et al.* 2001; Myers-Smith *et al.* 2015a).

Shrub expansion may affect climate by altering the surface energy budget (e.g. decrease surface albedo) and the carbon cycle (e.g. decrease methane emission by permafrost thawing protection through shading) among others (Eugster *et al.* 2000; Chapin 2003; Beringer *et al.* 2005). These shrub effects can be direct, through denser shrub cover and plant trait changes (Epstein *et al.* 2012; Juszak *et al.* 2016), but they can also be indirect by shifting community composition and diversity. Negative effects of shrub expansion on other plant functional types through resource competition and modification of local soil conditions may change community composition and diversity (Cornelissen *et al.* 2001; Startsev, Lieffers & Landhäusser 2008; Odland, Reinhardt & Pedersen 2015). Therefore, a better understanding of mechanisms driving shrub expansion is fundamental to improve the robustness of projected shifts in tundra vegetation, ecosystem processes, and regional climate in the Arctic. During the last decades, dendroecological methods have been adapted to shrub species to analyse shrub growth and expansion drivers in tundra ecosystems (Rayback & Henry 2005; Liang & Eckstein 2009; Schweingruber *et al.* 2013; Myers-Smith *et al.* 2015b). However, a synthesis on climate sensitivity of arctic and alpine shrub growth summarizing the conducted dendroecological studies, revealed a very low number of studies in Russian arctic tundra, with only five locations available (Myers-Smith *et al.* 2015a).

In this study, we explored the effects of soil warming and nutrient addition on tundra shrub growth. We hypothesized that under simulated environmental conditions expected with climate warming (i.e. increasing soil temperature and nutrient availability) (i) arctic shrubs will grow faster and taller and (ii) bark investment will decrease promoted by a faster growth strategy in soil heated and fertilized plots. To test our hypotheses we run a soil warming and fertilization experiment in northeastern Siberia and measured growth ring widths of the four years before the

experiment and the four experimental years, height, wood biomass, bark thickness, and bark investment in individuals of four tundra shrub species.

3.2 Material and methods

3.2.1 Study area and species

The study area is located in the Kytalyk nature reserve, in the Indigirka lowlands, Yakutia, northeast Siberia (70°49'N, 147°28'E, 10 m.a.s.l.), in the continuous permafrost arctic region. The mean annual air temperature is -13.1°C, with minimum monthly means of -33.5°C in January and maximum of 11.3°C in July, and the mean annual precipitation is 210 mm (1980–2013, WMO station 21946, Chokurdakh, monthly summaries of GHCN-D, NOAA National Climatic Data Center), which mainly occurs during the growing season months (about mid-June to end-August). The experimental plots were placed on a tussock-sedge tundra area, which has a mean active layer thickness of 35 cm at mid-growing season and about 50 cm by the end of the season. The main vegetation comprises sedges (mainly *Eriophorum vaginatum*), abundant deciduous and evergreen dwarf shrubs, bryophytes and lichens, and has a maximum canopy height of 25 cm (Iturrate-Garcia *et al.* 2016).

We studied four shrub species: *Betula nana* ssp. *exilis* (Sukazcev) Hultén, *Ledum palustre* ssp. *decumbens* (Aiton) Hultén, *Salix pulchra* Cham., and *Vaccinium vitis-idaea* L. However, *L. palustre* was not included in the growth rate analysis because growth rings of this species were undistinguishable.

3.2.2 Experimental design and sampling

We run a fully factorial soil warming and fertilization experiment from 2011 to 2014 in the study area. The experiment had five blocks and two treatments (soil warming and fertilization) applied to six plots of 1.5 × 1.5 m placed at randomly chosen locations within each block. We randomly assigned the six treatment combinations (3 soil warming × 2 fertilization treatments) to the plots within blocks. Heating cables powered by solar panels were buried at 15 cm depth to rise soil temperature, which increased by 1.0°C at 15 cm depth during the growing season (Appendix 4, Table A4.1). We included a cable without heating to account for possible disturbance effects caused by burying the cables. In total, we had three warming treatments: no cable, unheated cable, and heated cable. For the nutrient addition treatment, we applied slow-release NPK

fertilizer tablets with micronutrients (Osmocote Exact Tablet, Scotts International, Heerlen, the Netherlands) at the start of the experiment and two years later. The fertilization treatment was nutrient addition (5.6 g N, 1.4 g P and 3.7 g K m^{-2} y^{-1}) and no addition.

We followed the protocol described in Pérez-Harguindeguy *et al.* (2013) to sample and transport the plant samples. At mid-growing season, we randomly selected six healthy-looking individuals (< 20% leaf damage) of each species in every plot, except for *S. pulchra* for which fewer individuals were present (one to four individuals per plot). We sampled the root collar of the selected individuals, after measuring shrub height, and preserved the samples in ethanol (40% vol. aquous solution) until laboratory processing.

3.2.3 Height, wood biomass and wood fraction

We measured shrub height before individual sampling as the vertical distance from the tallest vegetative tissue of each individual to the ground.

We separated main stem and branches from other aboveground structural parts and weighed them before (wet weight) and after oven-drying (dry weight, 60°C, 72 h). Aboveground wood biomass was the sum of stem and branch dry weights. To estimate wood fraction, we divided aboveground wood biomass dry weight by dry weight of all aboveground structural parts (total aboveground biomass).

3.2.4 Shrub growth rate

Thin sections of 20-30 μm were obtained using a GSL1 sledge microtome (Gärtner, Lucchinetti & Schweingruber 2014) from disks cut along the root collar of the main stem. We put the sections on microscope slides, adding a drop of glycerine:distilled water mixture (4:1). We used a camera AxioCam MRc connected to an Axioskop2 plus microscope (Carl Zeiss Microscopy GmbH, Jena, Germany) to photograph the samples with a 200× magnification and measure the annual growth ring widths in the pictures using the software AxioVision SE 64 v4.8.4. Due to the eccentricity of the slices, growth ring widths were measured along the longest axis of the slice (Fig. 3.1). Shrub growth rate was the average annual growth ring width of the four years previous to the experiment (growth rate before experiment) or the four experimental years (growth rate during experiment).

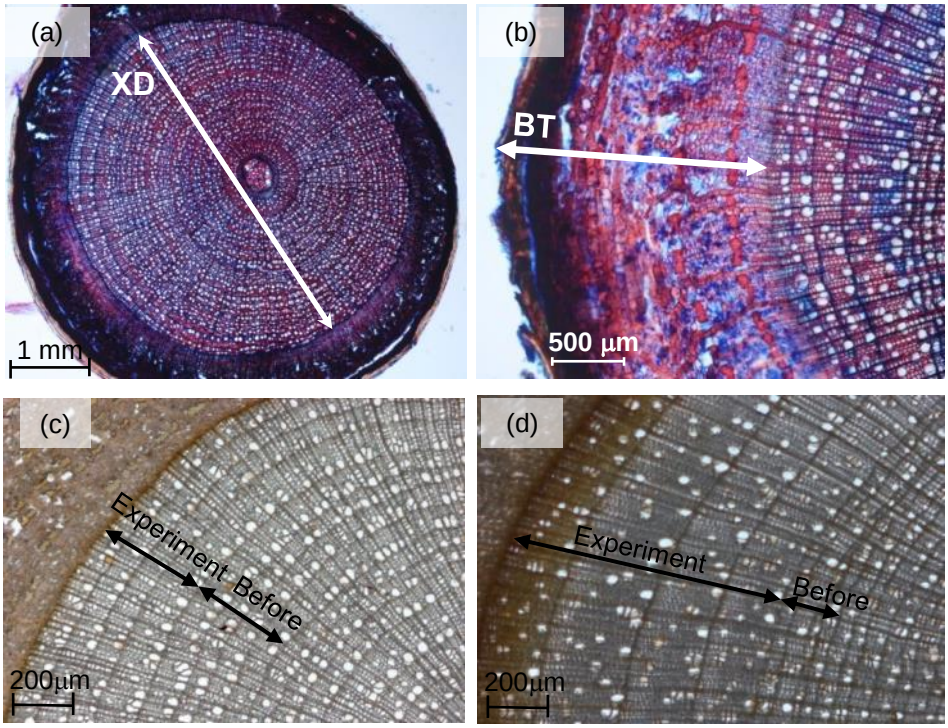

Figure 3.1: *Salix pulchra* slices showing xylem diameter (XD) (a), bark thickness (BT) (b), and growth ring width of the four years previous to the experiment and the four years of experiment in a control plot (c) and in a treatment plot (soil warming × fertilization) (d).

3.2.5 Stem traits

To measure the xylem diameter and bark thickness, we used the same slices and set-up as for the shrub growth rate. In this case, pictures were taken with a 10× magnification (50× for *V. vitis-idaea)*. We measured the xylem diameter along the longest axis of the slice (Fig. 3.1). Bark thickness was estimated by averaging the measurements taken along three different radii for each slice (Fig. 3.1). We divided the bark thickness by the xylem radius to obtain the bark investment.

3.2.6 Data analysis

The data analysis was performed using R.3.2.5. (http://r-project.org).

To test whether shrub growth was affected by soil warming and fertilization treatments, we analysed growth rate as a function of treatments, species, and their interaction with a linear mixed-effect model in asreml (ASReml, 3.0, VSN International Ltd., UK). Mean growth rate of the experimental years was log-transformed to account for size differences among species. The

fixed terms of the model were block (factor with five levels), log-transformed mean growth rate of the four years previous to the experiment (allometric correction standardizing the response variable by individual size within species), and the interaction among warming treatment, fertilization treatment and species. Random terms were plot (factor with 30 levels) and the interaction of plot and species. Soil warming and cable disturbance effects were tested by splitting the three-level warming factor into two contrasts of one degree of freedom (i.e. presence of cable and heating). We tested soil warming effects by fitting cable followed by heating and cable effects by fitting heating followed by cable. To test for significant differences between growth rates before and during the experiment, we used a general linear model univariate analysis of variance (ANOVA).

To explore the relationship of bark thickness and growth rate with shrub age – using xylem diameter as a proxy of age – and between bark investment and growth rate, we used a similar linear mixed-effect model to the one used to test the treatment effects on growth rate, but without applying the allometric correction. Outliers were detected based on model residual values more than three times and a half the median absolute deviation. We removed the outliers prior to analysing the significance of the linear relationships between variables using Pearson's correlation coefficients in addition to the linear mixed-effect models.

3.3 Results

3.3.1 Growth rate

Growth rate responded to fertilization, but not to soil warming (Fig. 3.2). Neither the interaction between treatments nor the disturbance caused by the buried cables was significant for shrub growth rate. The net effect of nutrient addition was a significant increase of the growth rate of *B. nana* ($F_{1,29} = 21.2$, $P < 0.001$), *S. pulchra* ($F_{1,29} = 16.2$, $P < 0.001$), and *V. vitis-idaea* ($F_{1,29} = 9.8$, $P < 0.01$) (Fig. 3.2). Mean growth rate during the experiment for every species and treatment is provided in Table 3.3.

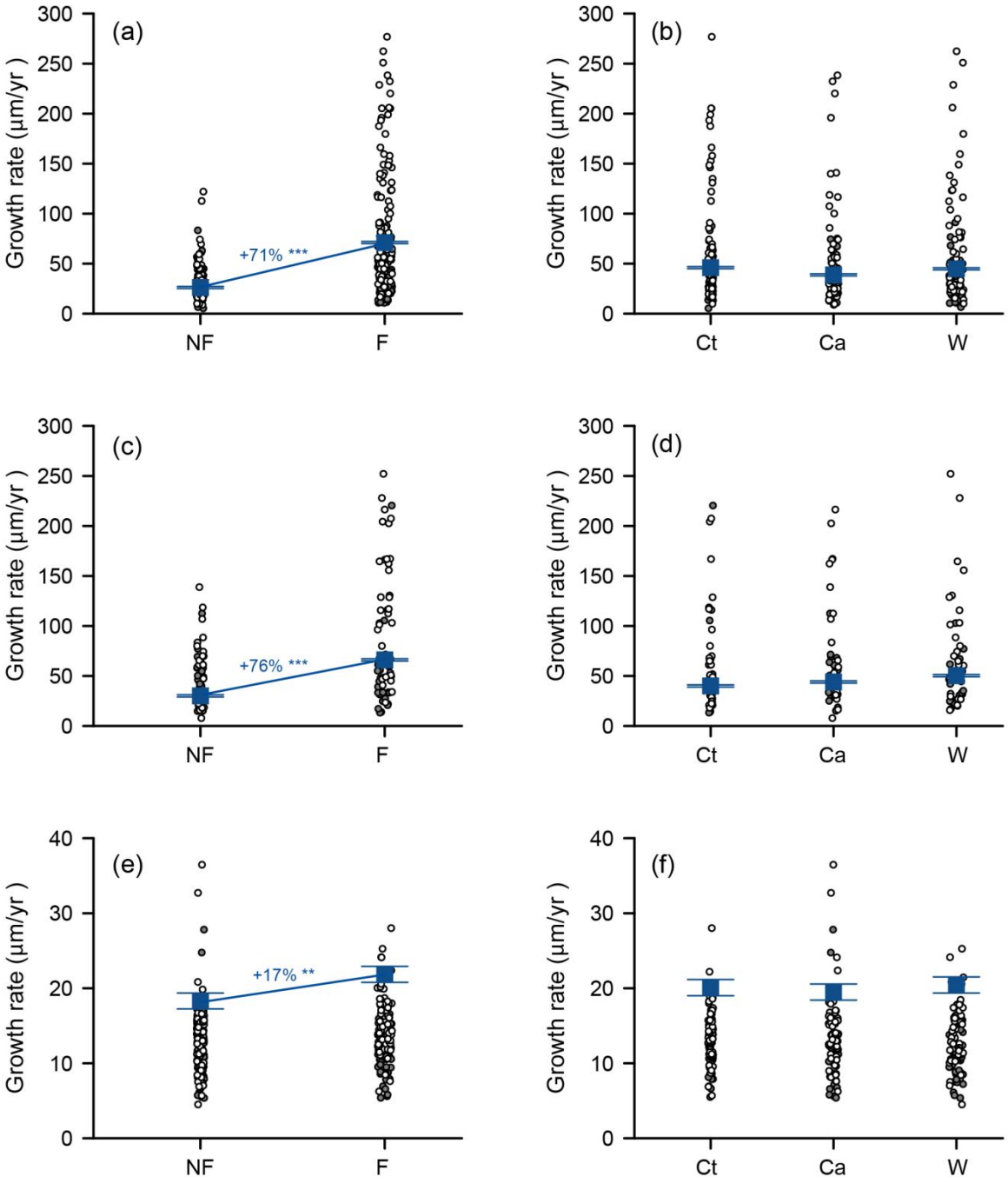

Figure 3.2: Net effect of fertilization treatment (left) and warming treatment (right) on the growth ring width of the four experimental years for *Betula nana* (a, b), *Salix pulchra* (c, d), and *Vacinium vitis-idaea* (e, f). Only fertilization net effect was significant (*** $P < 0.001$, ** $P < 0.01$). Circles show measured growth rates before the experiment (grey circles) and during the experiment (open circles). Black squares show predictions of the model for each treatment and error bars, the standard error of the predictions. The fertilization treatment levels are no nutrient addition (NF) and nutrient addition (F), and the warming treatment levels are no cable (Ct), unheated cable (Ca), and heated cable (W).

During the four experimental years, the mean growth rate increased as compared to the four years before the experiment for *B. nana*, *S. pulchra*, and *V. vitis-idaea* (Fig. 3.3). However, this increase was significant only in the fertilized plots (Fig. 3.3).

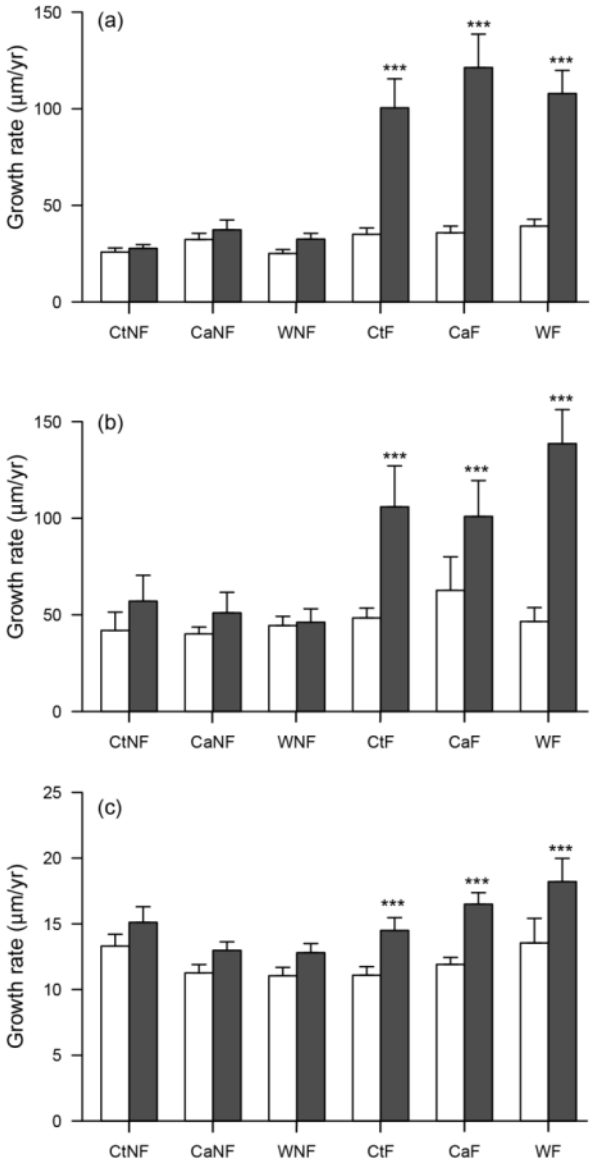

Figure 3.3: Mean growth rate of the four years before the experiment (white bars) and the four years of experiment (grey bars) of *Betula nana* (a), *Salix pulchra* (b), and *Vaccinium vitis-idaea* (c). The treatment combinations are no-nutrient addition × no-cable (CtNF), no-nutrient addition × unheated cable (CaNF), no-nutrient addition × heated cable (WNF), nutrient addition × no-cable (CtF), nutrient addition × unheated cable (CaF), and nutrient addition × heated cable (WF). Error bars indicate the standard error (n = 5 blocks). Significant differences in the growth rate of the years before and during the experiment are indicated by asterisks ($P < 0.001$).

3.3.2 Bark thickness and investment

Bark thickness decreased with the treatment combination (heated cables × nutrient addition) for *B. nana* (24% decrease, $F_{1,25} = 4.54$, $P < 0.05$) and *L. palustre* (25% decrease, $F_{1,25} = 8.15$, $P < 0.01$). Effects of soil heating or nutrient addition on bark thickness and bark investment were not significant (Table 3.2).

Shrub bark thickness was positively related to xylem diameter for *B. nana, S. pulchra*, and *V. vitis-idaea* (Fig. 3.4). This relationship was also significant and positive for *L. palustre* ($r = 0.663$, $P < 0.001$). Although weak, we found a negative correlation between bark investment and growth rate for *B. nana* and *V. vitis-idaea*, but not for *S. pulchra* (Fig. 3.4). These relationships were similar in plots with and without nutrient addition. Bark thickness, bark investment, and xylem diameter mean values are provided in Table 3.3.

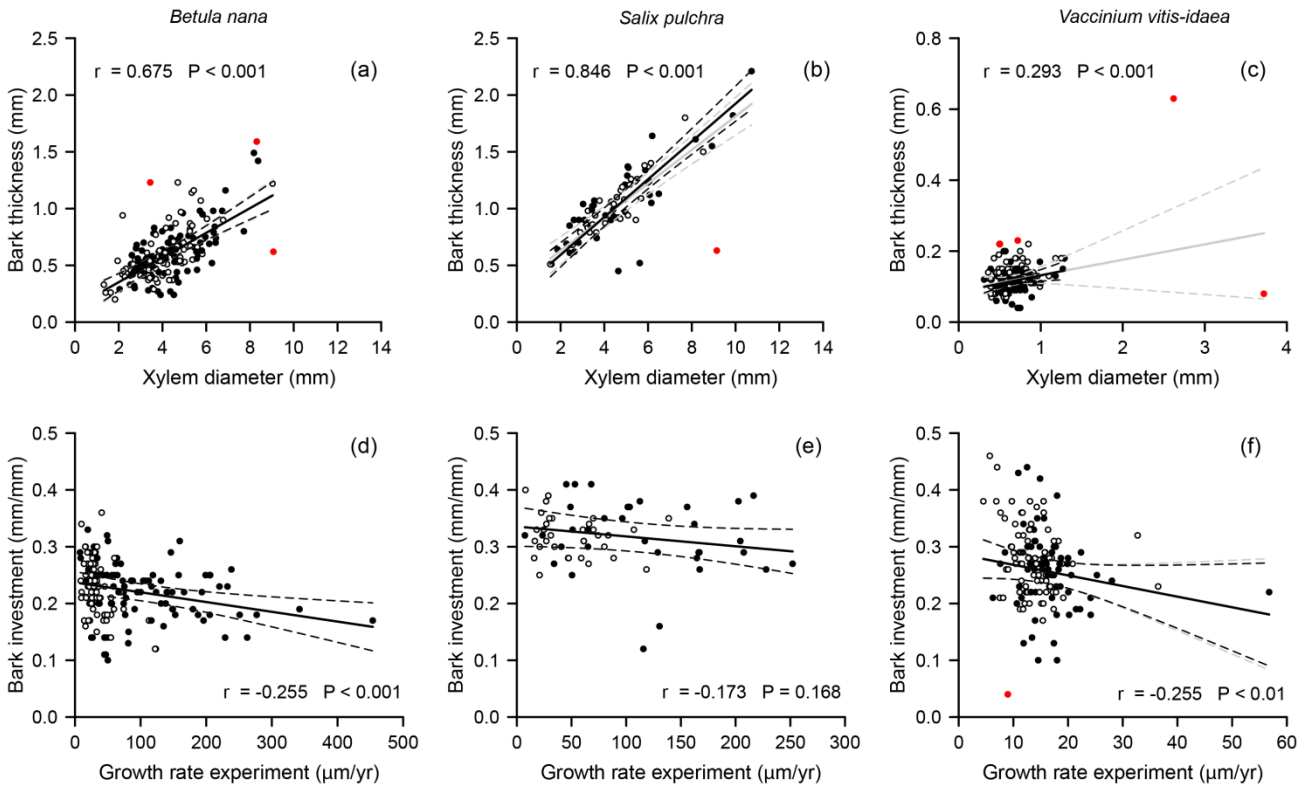

Figure 3.4: Correlations between bark thickness and xylem diameter (a-c) and bark investment and growth rate of the years of experiment (d-f) for *Betula nana*, *Salix pulchra*, and *Vaccinium vitis-idaea*. White circles show values from unfertilized plots, black circles from fertilized plots, and red circles are outliers. Solid lines are the values predicted by the linear mixed-effect model and dashed lines are the upper and lower limits of the confidence interval; in black, predictions without outliers and in grey, with outliers. Pearson's correlation coefficient (r) and p-value (P) of data without outliers are indicated in each panel.

3.3.3 Other traits

Height of the four species increased with nutrient addition, while wood fraction decreased (Table 3.2). However, wood fraction response to fertilization was statistically not significant for *V. vitis-idaea* (P = 0.099). Wood biomass of *L. palustre* was negatively affected by the disturbance of the buried cables (46% decrease, $F_{1,25} = 10.6$, $P < 0.01$). Xylem diameter of *V. vitis-idaea* was also affected by this disturbance, but only in the fertilized plots (9% increase, $F_{1,25} = 5.43$, $P < 0.05$). For the rest of traits, cable disturbance and treatment combination effect (heating × nutrient addition) were not significant. Trait mean values for each species and treatment are provided in Table 3.3.

Table 3.2: Effects of cable disturbance (C), soil heating (H), and fertilization (F) on structural and stem traits of each shrub species (*B. nana* (Betn), *S. pulchra* (Salp), *L. palustre* (Ledp) and *V. vitis-idaea* (Vacv)). Positive effect indicates increasing trait value with the treatment and negative effect decreasing value. Significant effects are in bold. Effect of the soil heating and fertilization treatment combination was not included as it was significant only for bark thickness of Betn and Ledp (see section '3.3 Results').

	Betn		Salp		Ledp		Vacv	
	Effect %	$F_{1,28}$	Effect %	$F_{1,28}$	Effect %	$F_{1,28}$	Effect %	$F_{1,29}$
Height								
C	+ 3	0.2	+ 5	0.1	- 2	0.1	+ 15	3.34
H	+ 9	1.2	+ 5	0.2	+ 8	2.4	+ 6	0.54
F	**+ 47**	**37.2*****	**+ 34**	**12.3** **	**+ 27**	**34.1*****	**+ 40**	**42.1*****
Wood biomass								
C	- 30	0.24	- 8	0.79	**- 46**	**10.6****	+ 34	1.13
H	+ 33	0.91	+ 7	0.86	+ 47	3.96	+ 19	0.41
F	+ 48	2.61	+ 13	0.64	+ 3	0.04	+ 61	4.34
Wood fraction								
C	- 2	0.58	+ 6	3.57	- 9	2.01	+ 12	0.35
H	+ 2	0.60	+ 1	0.01	- 1	0.01	- 6	0.24
F	**- 8**	**12.4****	**- 6**	**7.01***	**-11**	**5.74****	+ 13	2.99
Xylem diameter								
C	+ 1	0.01	+ 12	1.07	0	0.00	- 6	0.93
H	- 1	0.02	- 2	0.01	+ 7	1.80	+ 4	0.33
F	+ 12	3.69	+ 5	0.23	+ 4	0.75	0	0.01
Bark thickness								
C	- 3	0.14	+ 9	0.52	- 4	0.24	+ 4	0.19
H	- 9	1.46	- 11	1.08	- 3	0.08	- 6	0.35
F	+ 1	0.03	- 1	0.05	+ 3	0.13	- 9	1.20
Bark investment								
C	- 4	0.29	- 1	0.03	- 4	0.22	+ 8	0.35
H	- 7	1.18	- 8	0.95	- 8	0.63	- 7	0.37
F	- 7	1.84	- 5	0.42	- 1	0.02	- 6	0.39

Table 3.3: Growth rate during experiment, structural trait, and stem trait means (standard error) for each species (*B. nana* (Betn), *S. pulchra* (Salp), *L. palustre* (Ledp), and *V. vitis-idaea* (Vacv)) and treatment combination (no-cable (Ct), unheated cable (Ca), heated cable (W), no nutrient addition (NF), and nutrient addition (F)).

	CtNF	CaNF	WNF	CtF	CaF	WF
Growth rate ($\mu m \cdot yr^{-1}$)						
Betn	27.7 (2.0)	37.3 (5.1)	32.5 (3.0)	100.5 (15.0)	121.3 (17.3)	107.9 (12.0)
Salp	57.1 (13.4)	51.0 (10.6)	46.2 (6.9)	105.9 (21.2)	100.9 (18.6)	138.6 (17.6)
Vacv	15.1 (1.2)	13.0 (0.6)	12.8 (0.7)	14.5 (1.0)	16.5 (0.9)	18.2 (1.8)
Height (cm)						
Betn	13.6 (1.0)	13.5 (0.7)	14.3 (0.9)	19.0 (1.2)	18.9 (0.8)	22.3 (1.2)
Salp	14.9 (1.1)	14.6 (1.3)	14.9 (1.4)	18.1 (1.6)	18.8 (2.1)	20.9 (1.7)
Ledp	11.8 (0.8)	10.9 (0.6)	11.3 (0.7)	13.3 (0.6)	13.7 (0.6)	15.7 (0.8)
Vacv	3.6 (0.3)	4.1 (0.2)	4.1 (0.2)	5.2 (0.4)	6.0 (0.4)	6.5 (0.3)
Wood biomass (g)						
Betn	2.3 (0.6)	2.8 (0.7)	2.9 (0.6)	6.1 (1.4)	2.4 (0.6)	3.9 (1.0)
Salp	4.4 (0.8)	2.7 (0.8)	1.8 (0.5)	2.6 (0.9)	3.4 (1.0)	4.6 (1.3)
Ledp	1.01 (0.20)	0.49 (0.10)	1.1 (0.3)	1.4 (0.4)	0.94 (0.33)	0.74 (0.15)
Vacv	0.02 (0.00)	0.02 (0.00)	0.02 (0.00)	0.02 (0.00)	0.04 (0.01)	0.06 (0.01)
Wood fraction ($g \cdot g^{-1}$)						
Betn	0.79 (0.04)	0.54 (0.03)	0.54 (0.03)	0.52 (0.02)	0.53 (0.02)	0.53 (0.02)
Salp	0.76 (0.04)	0.53 (0.03)	0.61 (0.03)	0.52 (0.02)	0.56 (0.03)	0.54 (0.03)
Ledp	0.45 (0.01)	0.48 (0.03)	0.50 (0.04)	0.46 (0.01)	0.44 (0.02)	0.43 (0.01)
Vacv	0.52 (0.05)	0.51 (0.05)	0.51 (0.05)	0.53 (0.06)	0.52 (0.05)	0.52 (0.04)
Xylem diameter (mm)						
Betn	3.86 (0.25)	4.13 (0.32)	4.04 (0.21)	4.59 (0.28)	4.46 (0.28)	4.18 (0.17)
Salp	4.91 (0.44)	4.44 (0.54)	4.15 (0.30)	4.04 (0.50)	5.42 (0.79)	5.25 (0.53)
Ledp	2.80 (0.17)	2.81 (0.17)	3.22 (0.21)	3.06 (0.19)	3.07 (0.25)	3.01 (0.18)
Vacv	0.85 (0.12)	0.61 (0.03)	0.65 (0.04)	0.62 (0.03)	0.68 (0.03)	0.69 (0.04)
Bark thickness (mm)						
Betn	0.57 (0.05)	0.61 (0.05)	0.64 (0.04)	0.71 (0.04)	0.64 (0.04)	0.49 (0.03)
Salp	1.13 (0.10)	1.01 (0.08)	0.96 (0.05)	0.95 (0.07)	1.23 (0.13)	0.99 (0.10)
Ledp	0.18 (0.01)	0.17 (0.01)	0.19 (0.01)	0.19 (0.01)	0.21 (0.01)	0.16 (0.01)
Vacv	0.14 (0.02)	0.12 (0.01)	0.13 (0.01)	0.11 (0.00)	0.13 (0.01)	0.11 (0.01)
Bark investment ($mm \cdot cm^{-1}$)						
Betn	0.23 (0.01)	0.24 (0.01)	0.24 (0.01)	0.24 (0.01)	0.22 (0.01)	0.19 (0.01)
Salp	0.32 (0.01)	0.32 (0.01)	0.32 (0.01)	0.34 (0.01)	0.32 (0.01)	0.28 (0.02)
Ledp	0.12 (0.00)	0.11 (0.01)	0.11 (0.00)	0.11 (0.00)	0.12 (0.00)	0.10 (0.01)
Vacv	0.26 (0.01)	0.29 (0.01)	0.29 (0.01)	0.26 (0.01)	0.28 (0.01)	0.24 (0.02)

3.4 Discussion

We explored the effects of soil warming and increased nutrient availability on radial and vertical growth, wood biomass, and bark thickness and investment of four tundra shrub species. Our findings show that all the species grew faster (radially and vertically) with nutrient addition, but not with soil warming contrary to our hypothesis. We also found a negative effect of the treatment combination (heated cables × nutrient addition) on age-dependent bark thickness and a negative correlation between bark investment and growth rate of some of the species. Shrub response to the treatments was different among species, especially between deciduous and evergreen species. These results suggest that shrubs, especially deciduous species, will grow faster and taller in a changing climate, but might be more vulnerable to pests, herbivory, and climate extremes (e.g. frost events, drought).

3.4.1 Dendroecology in arctic tundra

Dendroecological approaches have been adapted and increasingly applied to arctic tundra shrubs in order to explore their sensitivity to climate (Woodcok & Bradley 1994; Bret-Harte, Shaver & Chapin 2002; Schweingruber & Poschlod 2005; Bär, Bräuning & Löffler 2006). However, shrub growth rings can be difficult to identify due to eccentric growth, narrow growth ring widths, and wedging, incomplete, or missing rings, which can lead to erroneous results (Myers-Smith *et al.* 2015b). Furthermore, these approaches are mainly observational (dendrochronology) and therefore difficult to discern whether the correlation between growth and climatic factors is driven by direct effects of the factor or by other mechanisms associated to its indirect effects (Buchwal et al., 2013; Hallinger et al., 2010; Hollesen et al., 2015; Liang and Eckstein, 2009; see exceptions: Bret-Harte et al., 2002; Rixen et al., 2010). Here, we combined dendroecological and experimental approaches to identify drivers of shrub growth. This combination requires the identification of fewer growth rings than for dendrochronology (only growth rings of the experimental years and the same number of years before the experiment). Thereby, analysing time will shorten and the probability of finding missing, incomplete or wedging rings may decrease. Moreover, the experimental design allows us to identify the actual drivers of shrub growth among the manipulated environmental factors.

3.4.2 Shrub growth under climate warming

We hypothesized that soil warming and fertilization would increase shrub radial growth. However, our findings showed that shrub growth responded to enhanced nutrient availability,

but not to soil warming. Similar effects were observed on the vertical growth of the four shrub species. Shrub growth unresponsiveness to soil warming might be explained by the treatment strength. The heating cables were buried deeper (~ 15 cm) than the depth where most of the root biomass of the study shrub species occurs (Churchland *et al.* 2010; Wang *et al.* 2016), resulting in a no significant increase of soil temperature (by less than 0.6°C) in the shrub root layer. Although shrubs can respond rapidly to environmental changes and some studies reported positive growth responses in four-year experiments, the short term of our experiment might additionally contribute to explain the lack of growth response to soil warming (Arft *et al.* 1999; Bret-Harte *et al.* 2002; Hallinger & Wilmking 2011). Moreover, we found that the effect of soil warming and nutrient addition treatment combination was not significant. This lack of significance suggests that treatment effects are additive and that shrub growth is co-limited by soil temperature and nutrient availability or limited by the indirect effect of soil temperature on nutrient availability (DeMarco *et al.* 2014).

Previous dendroecological studies in the area revealed early summer temperature as the most important factor influencing the annual growth variation in *B. nana* and *S. pulchra* (Blok *et al.* 2011a; Li *et al.* 2016). Several reasons might explain the discrepancy between those studies and our results. Firstly, we consider soil temperature instead of air temperature that may result in different responses (Weih & Karlsson 2001). Secondly, our experimental design allowed us to investigate only short-term responses of shrubs to increasing temperature that may differ from long-term responses, such as the ones investigated in those studies (Chapin *et al.* 1995; Boelman *et al.* 2003). Thirdly, we analysed the data using linear mixed-effect models (LMM), which can account for temporal variance in growth within individuals and temporal heterogeneity in growth patterns of different individuals (Lapointe-Garant *et al.* 2010; Myers-Smith *et al.* 2015a), instead of correlations that are normally used in dendrochronology. When Myers-Smith et al. (2015a) analysed data from our study area (Blok et al., 2011a) using LMM, *B. nana* radial growth was not statistically related to early summer temperature anymore. Lastly, the positive correlation between air temperature and shrub growth found in the dendrochronological studies might be explained by indirect effects of air temperature (Weih & Karlsson 2001). Rising air temperature can increase soil temperature, permafrost thawing, and soil organic matter mineralization, enhancing in both cases the nutrient availability (Schmidt *et al.* 1999; Walther *et al.* 2002; Schuur *et al.* 2009). However, these indirect effects are difficult to identify in the dendrochronological studies, because only temporal series of air temperature are used, but not series of soil temperature, active layer thickness or soil nutrient concentrations.

3.4.3 Bark thickness and investment

Shrub woody tissues conduct and store water and nutrients, provide biomechanical support, and, especially the bark, play an important role in the defence against frost damage, drought, herbivory, and pathogens (Kozlowski 1992; Rowe & Speck 2005; Paine *et al.* 2010; Lens *et al.* 2011). We found a positive correlation (< 1) between shrub bark thickness and xylem diameter for all the species, showing that bark thickness is age-dependent and that species bark investment is lower with age (Poorter *et al.* 2014). Bark thickening with age suggests that older individuals may be better protected and therefore can allocate more resources to functions other than defence (e.g. growth, reproduction) than younger ones (Payette, Delwaide & Simard 2010; Arco Molina *et al.* 2016).

Tundra shrubs are expected to invest in growth, as indicated by our results, allocating fewer resources to defence with climate warming (Westoby *et al.* 2002; Grime 2006; Reich 2014). Therefore, tundra shrubs might reduce their stress resistance as a consequence of the growth–defence trade-off (Chapin *et al.* 1993; Chave *et al.* 2009). The lower defence investment of shrubs is reflected in the bark thickness decrease with the treatment combination (soil heating × nutrient addition), which was likely driven by a larger warming response in the presence of nutrients. Similar effects were found on *B. nana* bark investment. Moreover, bark investment and growth rate were negatively correlated, though weakly, for *B. nana* and *V. vitis-idaea.* These bark responses may result in a lower defence of shrubs with climate warming in the short-term.

3.4.4 Shrub growth–climate feedbacks

Climate warming will enhance nutrient availability for vegetation in the Arctic through permafrost thawing, which will mobilize nutrients trapped in the permafrost, and higher soil organic matter mineralization rates (Schmidt *et al.* 1999; Walther *et al.* 2002; Schuur *et al.* 2009). Tundra shrub growth (vertical and radial) will increase with the nutrient availability, as indicated in our results. Furthermore, our findings show decreased shrub wood fraction with nutrient addition, suggesting that resources will be allocated to leaf production. Thereby, denser canopies and greater leaf to wood ratio are expected with climate warming. Denser canopies will reduce the albedo, especially during snow accumulation and melting periods (Beringer *et al.* 2005; Sturm *et al.* 2005; Loranty, Goetz & Beck 2011), and the amount of shortwave radiation transmitted to the soil surface (Eugster *et al.* 2000; Pearson *et al.* 2013). Changes of leaf to wood ratio will also affect the surface radiation partitioning, which might result in lower soil temperature and thicker active layer (Juszak *et al.* 2014). Additionally, faster growing shrubs

may outcompete other species through light and nutrients, especially cryptogam species, which might also affect the surface radiation budget and the water cycle (Cornelissen *et al.* 2001; Startsev *et al.* 2008; Odland *et al.* 2015).

3.5 Conclusions

In this study, we explored the effects of soil warming and increased nutrient availability on shrub growth, bark thickness, and bark investment by combining experimental manipulation of two suggested environmental drivers of shrub growth – soil temperature and nutrient availability – with dendroecology. Our results showed that shrub growth was mainly limited by nutrient availability and not by soil temperature, at least in the short-term, and that the responses were species-specific. Furthermore, the decrease of bark thickness and bark investment found for some of the species, suggests that shrubs might be more vulnerable to climate extremes (frost or drought events), herbivory, and pathogens under climate warming conditions. The combination of dendroecological and experimental methods, manipulating environmental factors in order to simulate projected climate scenarios for the Arctic (e.g. precipitation increase or snow layer decrease), together with increasing number of study shrub species and locations, might reduce the uncertainties related to shrub growth sensitivity to climate. In turn, the better understanding of shrub growth will provide insight into shrub–climate feedbacks in arctic tundra ecosystems.

3.6 Acknowledgements

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3.7 References

See thesis section ‘References’.

CHAPTER 4

Coordinated trait responses of tundra shrubs in a changing Arctic

"[...] everyone trusts an observation

except the person who made it"

(Harlow Shapley)

Coordinated trait responses of tundra shrubs in a changing Arctic

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Abstract

Air temperature is increasing and will keep rising, more rapidly in the Arctic than in other regions. As a consequence, soil warming is expected, accelerating soil organic matter mineralization and enhancing in turn the nutrient availability for plants. These projected changes might affect plant diversity, traits, and strategies, altering ecosystem functioning and vegetation–climate interactions. Shrub expansion has been widely observed in the Arctic and attributed to climate warming. However, uncertainties related to shrub growth and trait sensitivity to climatic changes remain. Here, we explore the effects of soil warming and increased nutrient availability on growth, plant traits, and resource acquisition of tundra shrubs. We measured seventeen plant traits related to growth, biomass, structure, and the leaf economics spectrum in four shrub species in a soil warming and fertilization experiment in a Siberian tundra ecosystem. Nutrient addition and to a lesser extent soil warming, caused shrubs to grow faster, produce more biomass, and shift from resource conservation to faster resource acquisition. Although these changes will result in shrub expansion in the short term, the faster resource acquisition may enhance shrub vulnerability to pests and climate extremes, which are projected to become more frequent. Our findings suggest that plant traits of tundra shrubs respond in a coordinate way to environmental changes. Taking this coordinated response into account will contribute to more realistic dynamic global vegetation models and robust predictions of shifts in vegetation, climate–vegetation feedbacks, and ecosystem processes.

4.1 Introduction

Climate warming is unequivocally taking place, especially in the Arctic, where surface air temperature has risen more rapidly than in other regions over the past decades (IPCC 2013). Higher temperatures can cause changes in vegetation composition and distribution by direct effects or indirect effects like higher organic matter mineralization rates resulting in more mineral nutrients available to plants (Schmidt, Jonasson & Michelsen 1999; Epstein *et al.* 2000; Walther *et al.* 2002). In turn, changes in plant distribution, diversity, and traits such as growth, height or specific leaf area (Hudson, Henry & Cornwell 2011), will have consequences on the surface energy budget, and the water and carbon cycle that might feed back to the regional climate (Foley *et al.* 2003; Chapin *et al.* 2005; Pearson *et al.* 2013).

Plants use resources – nutrients, water, and light – in different ways to grow, reproduce, compete with neighbour plants, and defend themselves against pathogens and herbivores (plant strategies) (Bazzaz *et al.* 1987; Ordoñez *et al.* 2010). However, as resources are normally limited, plants are unable to perform well in all these functions simultaneously. Therefore, plants have to allocate the resources to one function versus another (trade-off) (Grime 1977; Westoby *et al.* 2002; Reich 2014). Environmental changes, such as the ones promoted by climate warming (e.g. increasing amount of resources available in the soil), may modify the strategies and trade-offs adopted by plants (Grime 2006; Ordoñez *et al.* 2010). Plant strategies and trade-offs can be identified by measuring plant traits and their correlations (Grime *et al.* 1997; Westoby *et al.* 2002). Plant traits also determine plant responses to environmental factors, affecting ecosystem processes and services (Lavorel & Garnier 2002; Kattge *et al.* 2011). Therefore, analysing plant trait responses to climate warming can give insight into future ecosystem functioning and structure changes (Díaz *et al.* 2007).

Tundra plants are adapted to short growing seasons and harsh environmental conditions, such as extremely low temperatures, precipitation, and soil nutrient availability (Billings & Mooney 1968; Crawford 2008). This adaptation is reflected in their conservative strategies (slow growth and high persistence and efficient use of nutrients) and plant traits (e.g. low height, small specific leaf area, and long leaf lifespan) (Chapin 1980a; Reich, Walters & Ellsworth 1997; Cornelissen 1999). The low rates of resource acquisition and tissue turnover of slow-growing species allow them to allocate resources to other processes, such as defence against pathogens and herbivores or storage, and confers plants stress resistance, especially in low-resource environments such as high-latitude ecosystems (Chapin, Autumn & Pugnaire 1993).

Vegetation distribution and plant traits are expected to respond to the environmental changes projected for the Arctic: increasing temperature and precipitation (~3°C and 20% under emission scenario RCP4.5), thawing permafrost, and higher nutrient availability (Richter-Menge & Overland, 2010; Elmendorf *et al.*, 2012; IPCC, 2013). For instance, tundra expansion (shrubification) is taking place in many arctic regions and is suggested to be driven by climate warming (Tape, Sturm & Racine 2006; Myers-Smith *et al.* 2011). Shrubification is spatially and temporally heterogeneous and may not occur everywhere in the Arctic (Myers-Smith *et al.* 2011; Tape *et al.* 2012; Bhatt *et al.* 2013; Kremers, Hollister & Oberbauer 2015). This heterogeneity can be attributed to differential growth strategies and sensitivity of shrubs to climate, in addition to variation of environmental factors across the Arctic (Blok *et al.* 2010; Kremers *et al.* 2015; Myers-Smith *et al.* 2015a). Shrub responses to climate can alter the surface energy budget and the carbon cycle among others, which in turn affect climate (Eugster *et al.*, 2000; Chapin, 2003; Beringer *et al.*, 2005; Juszak *et al.*, 2016). A better understanding of the mechanisms driving arctic shrubification and the shrub–climate interactions is fundamental to improve the accuracy of dynamic global vegetation models and predictions of vegetation shifts (Cramer *et al.* 2001; Doherty *et al.* 2010). However, despite increasing efforts, uncertainties related to shrub climate sensitivity and to direction and magnitude of feedbacks remain (Myers-Smith *et al.* 2015a). Experiments simulating future climatic conditions are useful to identify the drivers of vegetation change and increase the understanding of shrub–climate interactions (Elmendorf *et al.* 2012; Hollister *et al.* 2015).

In this study, we explored the consequences of soil warming and increasing nutrient availability on tundra shrub traits and trait coordination. We hypothesized that, under simulated future environmental conditions (i.e. increasing soil temperature coupled with nutrient availability enhancement), (i) arctic shrubs will change their growth strategy towards faster growing and will produce more biomass; (ii) shrubs will also change their resource acquisition trade-off from resource conservation to faster acquisition; (iii) the relationships among shrub structural traits and resource acquisition traits will change. To test our hypotheses, we run a soil warming and fertilization experiment in Siberia and measured seventeen plant traits related to growth (including growth ring width), biomass, and resource acquisition, as well as structural plant traits that might affect the radiation budget, in individuals of four tundra shrub species.

4.2 Materials and methods

4.2.1 Study area

The study area is located in the Yakutian nature reserve of Kytalyk, northeastern Siberia (70°49'N, 147°28'E, 10 m.a.s.l.), in the continuous permafrost arctic region. The mean annual air temperature is -13.1°C, with minimum and maximum monthly means of -33.5°C in January and 11.2°C in July, and the mean annual precipitation is 210 mm (1980–2013, WMO station 21946, Chokurdakh, monthly summaries of GHCN-D, NOAA National Climatic Data Center). The experimental plots were placed on a tussock-sedge tundra area of organic and slightly acid soil (pH 6). The mean active layer thickness is 35 cm at mid-growing season and about 50 cm by the end. The main vegetation has a maximum canopy height of 25 cm and comprises sedges (mainly *Eriophorum vaginatum*), abundant deciduous and evergreen dwarf shrubs, bryophytes, and lichens (Iturrate-Garcia *et al*., 2016).

4.2.2 Experimental design

To address whether climate change might have effects on shrub plant traits, we run a soil warming and fertilization experiment from 2011 to 2014 on the study area. The experiment had a fully factorial block design with five blocks and combinations of two treatments (soil warming and fertilization) applied to six plots of 1.5 × 1.5 m placed at randomly chosen locations within each block. The six treatment combinations (3 soil warming × 2 fertilization treatments) were randomly assigned to the plots within blocks. We buried heating cables powered by solar panels, which increased growing season soil temperature by 1.0°C at 15 cm depth (Appendix 4, Table A4.1). The soil warming treatment consisted in no cable, unheated cable, and heated cable. The unheated cable plots served as reference for the soil warming treatment, while plots without cable were included to quantify possible disturbance effects of the cable alone. The fertilization treatment was nutrient addition and no addition. For the nutrient addition treatment, we applied slow-release NPK fertilizer tablets with micronutrients (Osmocote Exact Tablet, Scotts International, Heerlen, the Netherlands) at the start of the experiment and two years later. We added 5.6 g N, 1.4 g P, and 3.7 g K $\cdot$ m^{-2} $\cdot$ yr^{-1}.

4.2.3 Study species and sampling

We studied four shrub species present in all experimental plots: *Betula nana* ssp. *exilis* (Sukazcev) Hultén and *Salix pulchra* Cham., which are deciduous, and *Ledum palustre* ssp. *decumbens* (Aiton) Hultén and *Vaccinium vitis-idaea* L., which are evergreen (Fig. 4.1).

We followed the protocol described in Pérez-Harguindeguy *et al.* (2013) to sample and transport the plant samples. We randomly selected six healthy-looking individuals (less than 20% leaf damage) of each species per plot at mid-growing season, except for *S. pulchra* for which fewer individuals were present in the experimental plots. We cut the selected individuals below the root collar after measuring their height. Plant traits were measured in the laboratory within a few hours.

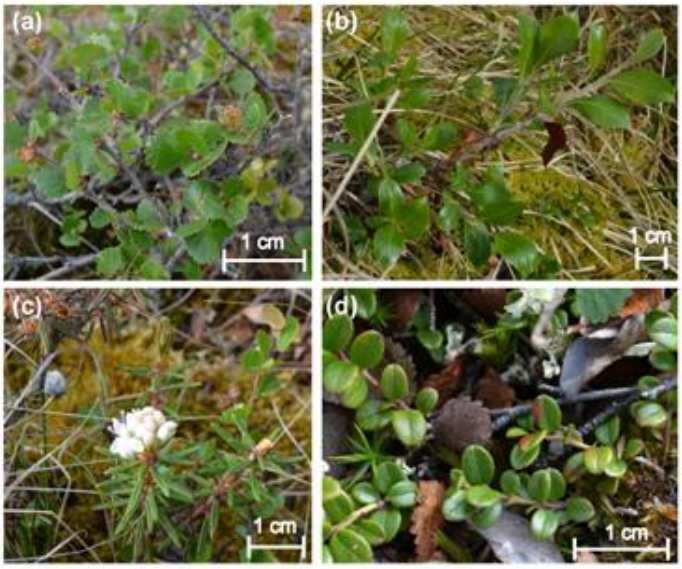

Figure 4.1: Study species: *Betula nana* (a), *Salix pulchra* (b), *Ledum palustre* (c), and *Vaccinium vitis-idaea* (d).

4.2.4 Plant traits

Height. Plant height was measured in the field as the vertical distance from the ground to the tallest vegetative tissue of the individual (maximum vegetative height).

Relative growth. We defined relative growth as the ratio of the growth ring width of the four years of experiment to the width of the four years previous to the experiment (values greater than the unit indicate faster growth with treatments). We cut thin sections of 20 – 30 μm along the root collar of each individual and placed them on microscope slides. We used a camera

AxioCam MRc connected to an Axioskop2 plus microscope (Carl Zeiss Microscopy GmbH, Jena, Germany) to photograph the samples with 200× magnification and measured growth ring widths using the software AxioVision SE 64 v4.8.4. Due to the eccentricity of the slices, we measured the growth ring width along the longest axis for three of the four species (*L. palustre* growth rings were undistinguishable).

Total aboveground, wood, and leaf biomass. We separated each sample into different structural parts (leaves, stem, branches, buds, and flowers) and weighed them before (wet weight) and after oven-drying (dry weight, 60°C, 72 h). Total aboveground biomass was calculated as dry weight of all the structural parts, and wood biomass as dry weight of the stem and branches. We divided wood and leaf biomass by the total aboveground biomass to determine the wood and leaf fraction.

Stem-specific density (SSD). We cut approximately 3-cm-long sections of the main stem at one third of the stem length. We measured the diameter and length of the stem sections, oven-dried (60°C, 72 h) and weighed them. SSD was determined by dividing the dry mass of a section by its volume.

Stem diameter and bark thickness. We used the same slices and set-up as for the relative growth trait to take pictures with 50× magnification for *V. vitis-idaea* and 10× for the other three species. Stem diameter was measured along the longest axis of the slices. Bark thickness was estimated as the average of the measurements taken along three different radii for each slice.

Leaf area (LA) and specific leaf area (SLA). We cut two leaves per individual, including the petiole, from the top and bottom canopy layers. We scanned the leaves with a flatbed scanner (LiDE 70 Canon Inc., Japan, 300 dpi image resolution) calibrated with a $1cm^2$ reference. Then, we estimated LA by counting pixels using the software MatLab R2014a (The MathWorks, Inc., MA, USA). We oven-dried the scanned leaves (60°C, 72 h) and weighed them to determine SLA by dividing the LA of each leaf by its dry weight.

Leaf dry matter content (LDMC). We followed a variation of the partial rehydration method to determine LDMC using the same leaves as for LA (Vendramini *et al.* 2002; Vaieretti *et al.* 2007). To assure maximum hydration, we cut whole individuals in the morning, wrapped the samples in moist paper, and put them in sealed plastic bags (Pérez-Harguindeguy *et al.* 2013). We kept the samples in the dark at low temperatures until they were weighed within the

following six hours. The individual leaves were re-weighed after oven-drying them (60°C, 72 h). LDMC was the dry mass of a leaf divided by its fresh mass.

Leaf nitrogen concentration (LNC). Oven-dried leaves were milled and leaf carbon and nitrogen concentrations determined by dry combustion (TruSpec Micro-CHN analyser, Leco Corporation, MI, USA) in samples of 2 mg. Then, the carbon to nitrogen ratio (C:N) was calculated.

Leaf phosphorus concentration (LPC). We used a colorimetric assay employing ammonium heptamolybdate to determine LPC. Milled samples of 0.05 g were combusted in a muffle furnace (B180 Nabertherm, Germany) programmed with one-hour heating up ramp to 600°C and two hours and a half at 600°C. We added 2 ml of 0.1 M H_2SO_4 to the ashes, followed by 5 ml of distilled water, and filtered the suspension (Macherey Nagel MN615). The phosphorus in the extracts was determined using a continuous flow analyser (Skalar Analytical B.V., the Netherlands) calibrated with KH_2PO_4 standards.

4.2.5 Statistics

All data were analysed using R 3.2.5 (http://r-project.org).

To test if shrub growth, aboveground biomass, and plant traits were affected by the soil warming and fertilization treatments, we analysed each plant trait as a function of treatments, species, and their interaction with a linear mixed-effect model fitted in asreml (ASReml 3.0, VSN International Ltd., UK). The fixed terms were block (factor with five levels), the interaction among warming treatment (three levels), fertilization treatment (two levels) and species (four levels), and the interaction between species and block (term recognised in the course of the statistical analysis to take into account the species trait differences among blocks). We fitted plot (factor with 30 levels) and the interaction of plot and species as random terms. We tested for soil warming and cable disturbance effects by splitting the three-level warming factor into two contrasts of one degree of freedom (i.e. presence of cable and heating). Cable effects were tested by fitting heating followed by cable, whereas soil warming effects were tested by fitting cable followed by heating. All plant trait data were log-transformed to account for the different species sizes, except leaf and wood fraction, C:N, and N:P. In addition, we also applied an isometric correction to the relative growth trait dividing the growth ring width of the four years of experiment by the width of the four years previous to the experiment to standardize by individual size within species.

In order to explore the shrub resource acquisition trade-off and its change with treatments, standardized plant traits data were subjected to principal component analysis (PCA; vegan package version 2.4-0; Oksanen 2016). We analysed the traits SLA, LA, LDMC, LNC, LPC, and C:N. We grouped the data in the PCA according to the fertilization treatment (nutrient addition and no addition) because of unresponsiveness of most of the traits to the soil warming treatment.

To test for changes of the relationship between structural traits and resource acquisition traits with nutrient addition, we used a linear mixed-effect model. We extracted the loadings of the first PC axis and then analysed the response variables (structural traits: height, SSD, wood biomass, wood fraction, stem diameter, and bark thickness) as a function of the interaction of the first PC axis loadings with the fertilization treatment (fixed term). Plot was considered as a random term. The structural trait values were log-transformed, except SSD and wood fraction, to reduce the variation due to different species sizes.

4.3 Results

4.3.1 Shrub growth and biomass

Shrub growth responded to fertilization, but not to soil warming (Table 4.2). The relative growth was faster in fertilized than in unfertilized plots. The total aboveground biomass responded positively to fertilization and also to soil warming (Table 4.2). This response was driven by increasing leaf and wood biomass in fertilized plots, but only leaf biomass in heated plots. In fertilized plots, the increase in leaf biomass was greater than for wood biomass, which is reflected in an increasing leaf, but decreasing wood fraction (Table 4.2). Neither the interaction between treatments nor the disturbance caused by the buried cables was significant for shrub growth and biomass (Table 4.2). Mean values for relative growth and biomass of each species are shown by treatment (Table 4.3).

Table 4.2. Effects of cable disturbance, soil heating, and fertilization on plant traits of the shrub species. Positive effect indicates increasing trait value with the treatment and negative effect decreasing value. Significant effects are in bold. The interaction between soil warming and fertilization treatments was not included as it was not significant.

		Cable		Heating		Fertilization	
	Units	Effect (%)	$F_{1,28}$	Effect (%)	$F_{1,28}$	Effect (%)	$F_{1,28}$
Relative growth	$\mu m \cdot \mu m^{-1}$	+ 11	1.47	+ 1	0.001	**+ 45**	**28.8** ***
Total aboveground biomass	g	- 15	3.78	**+ 22**	**5.08** *	**+ 33**	**12.6** **
Wood biomass	g	- 14	2.99	+ 21	3.89	**+ 29**	**8.90** **
Leaf biomass	g	- 13	2.86	**+ 20**	**4.88** *	**+ 56**	**32.9** ***
Leaf fraction	$g \cdot g^{-1}$	+ 1	0.70	- 1	0.71	**+ 8**	**4.40** *
Wood fraction	$g \cdot g^{-1}$	- 1	0.60	0	0.10	**- 7**	**7.90** **
Height	cm	+ 5	0.60	+ 7	3.50	**+ 40**	**93.4** ***
Stem-specific density	$g \cdot cm^{-3}$	- 3	0.46	- 1	0.04	- 6	2.47
Leaf dry matter content	$g \cdot g^{-1}$	- 2	0.31	- 2	0.44	**- 13**	**27.0** ***
Leaf area	cm^2	- 1	1.61	**+ 9**	**18.0** ***	**+ 38**	**333** ***
Specific leaf area	$cm^2 \cdot g^{-1}$	+ 1	0.00	+ 5	3.00	**+ 17**	**68.0** ***
Leaf nitrogen content	%	+ 1	0.00	+ 3	2.00	**+ 34**	**172** ***
Leaf phosphorus content	$mg \cdot g^{-1}$	0	0.17	**+ 12**	**5.24** *	**+ 34**	**64.4** ***
Leaf C:N	ratio	- 2	0.00	- 5	3.00	**- 24**	**114** ***
Leaf N:P	ratio	+ 2	0.20	- 3	0.70	+ 3	0.20

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$

4.3.2 Plant traits

The measured plant traits were affected by the fertilization treatment, except stem diameter, bark thickness, SSD, and N:P (Table 4.2). Only LA and LPC were also affected by soil warming. The disturbance caused by the buried cables was not statistically significant (Table 4.2).

Shrub height increased with nutrient addition (Table 4.2). Leaves in the fertilized plots had greater LA and SLA, higher leaf nutrient concentration, and lower LDMC and C:N than unfertilized leaves. Although LA was greater with soil warming, SLA remained unresponsive to

it (Table 4.2). Mean values for each species plant traits and treatment are provided in Tables 4.3 and 4.4.

Table 4.3: Plant trait means (standard error) for each species (*B. nana* (Betn), *S. pulchra* (Salp), *L. palustre* (Ledp), and *V. vitis-idaea* (Vacv)) and treatment interaction (no-cable (Ct), unheated cable (Ca), heated cable (W), no nutrient addition (NF) and nutrient addition (F)).

	CtNF	CaNF	WNF	CtF	CaF	WF
Relative growth ($\mu m \cdot \mu m^{-1}$)						
Betn	1.2 (0.1)	1.3 (0.2)	1.3 (0.2)	2.0 (0.3)	2.7 (0.4)	2.1 (0.2)
Salp	1.2 (0.2)	1.4 (0.4)	1.1 (0.2)	1.5 (0.2)	2.1 (0.4)	3.2 (0.7)
Vacv	1.2 (0.1)	1.2 (0.1)	1.2 (0.1)	1.3 (0.1)	1.3 (0.1)	1.4 (0.1)
Total aboveground biomass (g)						
Betn	2.8 (0.6)	3.5 (0.9)	3.4 (0.6)	7.7 (1.7)	3.3 (0.7)	5.2 (1.2)
Salp	5.4 (1.0)	3.3 (0.9)	2.3 (0.6)	3.4 (1.0)	4.4 (1.2)	5.9 (1.5)
Ledp	1.5 (0.3)	0.81 (0.15)	1.7 (0.3)	2.1 (0.6)	1.5 (0.4)	1.4 (0.2)
Vacv	0.14 (0.01)	0.13 (0.02)	0.12 (0.02)	0.11 (0.01)	0.19 (0.03)	0.33 (0.06)
Wood biomass (g)						
Betn	2.3 (0.6)	2.8 (0.7)	2.9 (0.6)	6.1 (1.4)	2.4 (0.6)	3.9 (1.0)
Salp	4.4 (0.8)	2.7 (0.8)	1.8 (0.5)	2.6 (0.9)	3.4 (1.0)	4.6 (1.3)
Ledp	1.01 (0.20)	0.49 (0.10)	1.1 (0.3)	1.4 (0.4)	0.94 (0.33)	0.74 (0.15)
Vacv	0.02 (0.00)	0.02 (0.00)	0.02 (0.00)	0.02 (0.00)	0.04 (0.01)	0.06 (0.01)
Leaf biomass (g)						
Betn	0.40 (0.05)	0.52 (0.11)	0.48 (0.07)	1.4 (0.2)	0.76 (0.14)	1.1 (0.2)
Salp	0.98 (0.22)	0.64 (0.14)	0.46 (0.13)	0.76 (0.15)	0.95 (0.24)	1.2 (0.2)
Ledp	0.46 (0.06)	0.31 (0.05)	0.59 (0.09)	0.73 (0.12)	0.56 (0.13)	0.59 (0.10)
Vacv	0.12 (0.01)	0.11 (0.02)	0.10 (0.02)	0.09 (0.01)	0.15 (0.02)	0.26 (0.05)
Height (cm)						
Betn	13.6 (1.0)	13.5 (0.7)	14.3 (0.9)	19.0 (1.2)	18.9 (0.8)	22.3 (1.2)
Salp	14.9 (1.1)	14.6 (1.3)	14.9 (1.4)	18.1 (1.6)	18.8 (2.1)	20.9 (1.7)
Ledp	11.8 (0.8)	10.9 (0.6)	11.3 (0.7)	13.3 (0.6)	13.7 (0.6)	15.7 (0.8)
Vacv	3.6 (0.3)	4.1 (0.2)	4.1 (0.2)	5.2 (0.4)	6.0 (0.4)	6.5 (0.3)
Stem-specific density ($g \cdot cm^{-3}$)						
Betn	0.87 (0.07)	0.82 (0.05)	0.78 (0.05)	0.71 (0.03)	0.70 (0.03)	0.69 (0.03)
Salp	0.80 (0.05)	0.75 (0.04)	0.90 (0.08)	0.76 (0.06)	0.80 (0.06)	0.71 (0.04)
Ledp	0.60 (0.02)	0.64 (0.04)	0.61 (0.05)	0.57 (0.02)	0.60 (0.02)	0.56 (0.02)
Vacv	1.01 (0.09)	0.88 (0.09)	0.95 (0.08)	1.03 (0.09)	0.91 (0.08)	0.91 (0.08)

Table 4.4: Leaf trait means (standard error) for each species (*B. nana* (Betn), *S. pulchra* (Salp), *L. palustre* (Ledp), and *V. vitis-idaea* (Vacv)) and treatment interaction (no-cable (Ct), unheated cable (Ca), heated cable (W), no nutrient addition (NF) and nutrient addition (F)).

	CtNF	CaNF	WNF	CtF	CaF	WF
Leaf dry matter content ($g \cdot g^{-1}$)						
Betn	0.55 (0.02)	0.55 (0.02)	0.54 (0.03)	0.47 (0.03)	0.42 (0.02)	0.46 (0.02)
Salp	0.55 (0.03)	0.48 (0.02)	0.48 (0.01)	0.44 (0.06)	0.46 (0.12)	0.43 (0.11)
Ledp	0.55 (0.01)	0.54 (0.01)	0.52 (0.01)	0.49 (0.05)	0.48 (0.06)	0.47 (0.03)
Vacv	0.53 (0.03)	0.53 (0.01)	0.53 (0.01)	0.48 (0.07)	0.50 (0.03)	0.44 (0.06)
Leaf area (cm^2)						
Betn	0.95 (0.03)	0.94 (0.03)	1.04 (0.04)	1.01 (0.03)	1.12 (0.04)	1.10 (0.05)
Salp	3.3 (0.2)	3.4 (0.3)	2.9 (0.2)	4.3 (0.3)	3.4 (0.27)	5.0 (0.5)
Ledp	0.27 (0.01)	0.24 (0.01)	0.30 (0.02)	0.43 (0.02)	0.42 (0.02)	0.45 (0.02)
Vacv	0.39 (0.01)	0.38 (0.02)	0.41 (0.02)	0.57 (0.04)	0.65 (0.03)	0.66 (0.03)
SLA ($cm^2 \cdot g^{-1}$)						
Betn	132.0 (3.4)	132.5 (3.8)	135.4 (3.7)	157.4 (5.8)	163.8 (6.5)	154.4 (4.8)
Salp	121.1 (4.8)	121.6 (4.4)	124.7 (4.0)	123.2 (6.0)	123.6 (6.6)	129.6 (6.0)
Ledp	50.8 (1.7)	54.0 (2.0)	59.2 (1.8)	61.6 (2.2)	59.6 (2.7)	65.0 (1.5)
Vacv	57.9 (2.6)	59.4 (2.0)	61.2 (3.1)	78.9 (3.5)	78.6 (3.2)	83.9 (3.1)
LNC (%)						
Betn	24.3 (0.6)	23.7 (1.0)	24. 6 (0.8)	32.4 (1.3)	34.6 (0.9)	31.6 (2.0)
Salp	18.0 (0.9)	15.3 (0.8)	16.5 (1.1)	22.7 (0.8)	21.4 (1.4)	22.9 (1.5)
Ledp	13.2 (0.3)	14.0 (0.5)	16.0 (1.5)	17.9 (0.7)	19.0 (0.8)	17.8 (0.6)
Vacv	7.3 (0.4)	7.7 (0.4)	8.4 (0.4)	9.9 (0.5)	11.0 (1.0)	12.1 (1.4)
LPC ($mg \cdot g^{-1}$)						
Betn	2.1 (0.1)	2.0 (0.2)	2.1 (0.1)	3.8 (0.3)	3.9 (0.3)	4.0 (0.4)
Salp	1.5 (0.1)	1.3 (0.1)	1.9 (0.3)	1.5 (0.2)	1.3 (0.1)	1.7 (0.2)
Ledp	0.88 (0.03)	1.03 (0.06)	1.2 (0.1)	1.3 (0.1)	1.3 (0.1)	1.4 (0.1)
Vacv	0.53 (0.03)	0.56 (0.03)	0.68 (0.07)	0.78 (0.06)	0.80 (0.10)	0.82 (0.06)
Leaf C:N						
Betn	20.6 (0.5)	21.7 (1.1)	20.5 (0.6)	15.9 (1.0)	14.4 (0.3)	17.0 (1.5)
Salp	27.0 (1.2)	32.2 (2.4)	27.8 (3.2)	21.6 (0.8)	23.2 (1.7)	23.2 (1.8)
Ledp	40.5 (1.0)	38.4 (1.5)	35.3 (1.7)	30.2 (1.0)	27.9 (1.3)	28.8 (1.2)
Vacv	70.3 (3.2)	67.6 (3.3)	62.0 (3.1)	53.2 (3.1)	50.0 (3.9)	46.1 (3.3)
Leaf N:P						
Betn	12.2 (0.6)	13.0 (1.1)	12.4 (0.8)	9.3 (0.7)	9.3 (0.6)	9.4 (1.2)
Salp	12.4 (0.8)	12.1 (1.0)	11.9 (1.3)	16.1 (1.3)	17.4 (1.4)	16.0 (2.3)
Ledp	14.9 (0.3)	13.9 (0.5)	14.1 (0.3)	14.5 (0.5)	15.1 (0.8)	13.3 (0.8)
Vacv	14.0 (0.4)	14.0 (0.7)	13.1 (0.8)	13.1 (0.5)	14.5 (1.1)	15.1 (1.6)

4.3.3 Resource acquisition traits

In the principal component analysis of traits, individuals were separated into plant functional types (deciduous and evergreen) by the first PC axis and into species within PFT by the second PC axis (Fig. 4.2). Both axes together explained 75% of the variation among individuals. The first PC axis was mainly related to LNC, C:N, SLA, and LPC, explaining 56% of the variation. The second PC axis explained 19% of the variation and was mainly related to LDMC and LA. Under nutrient addition, individuals of the four species decreased LDMC and C:N and increased SLA, LA (slightly in the case of *B. nana*), and the leaf nutrient content (especially *B. nana*).

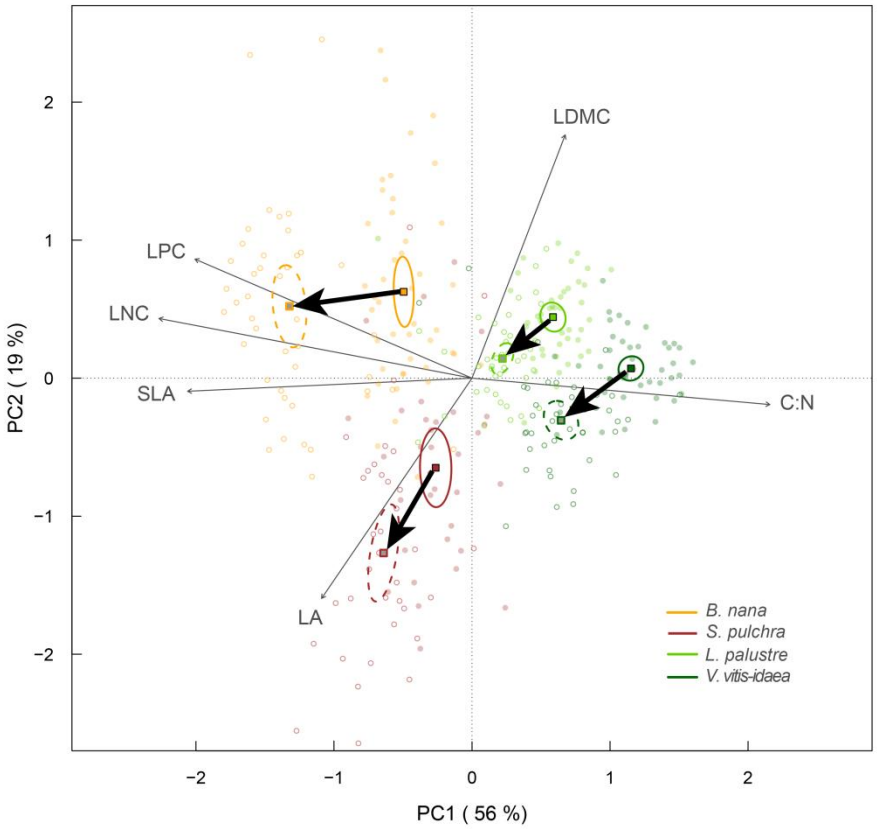

Figure 4.2: Principal component biplot of plant traits showing change in resource acquisition trade-off (black thick arrows) when nutrients are added. The plant traits included are leaf dry matter content (LDMC), carbon to nitrogen ratio (CN_ratio), leaf nitrogen content (LNC), leaf phosphorus content (LPC), specific leaf area (SLA), and leaf area (LA). Points are the trait scores of individuals without fertilization (closed circles) and with fertilization (opened circles). Sample scores are scaled by factor 15 and variable loadings by factor 7. Squares indicate the centre of the ordiellipses (standard error with 95% confidence interval) of the trait scores without nutrient addition (solid lines) and with nutrient addition (dashed lines). The first principal component explains 56% of the total variance, while the second component explains 19%.

4.3.4 Structural traits vs. resource acquisition traits

All the structural traits, except SSD, were negatively related with the first PC axis loadings (Fig. 4.3).

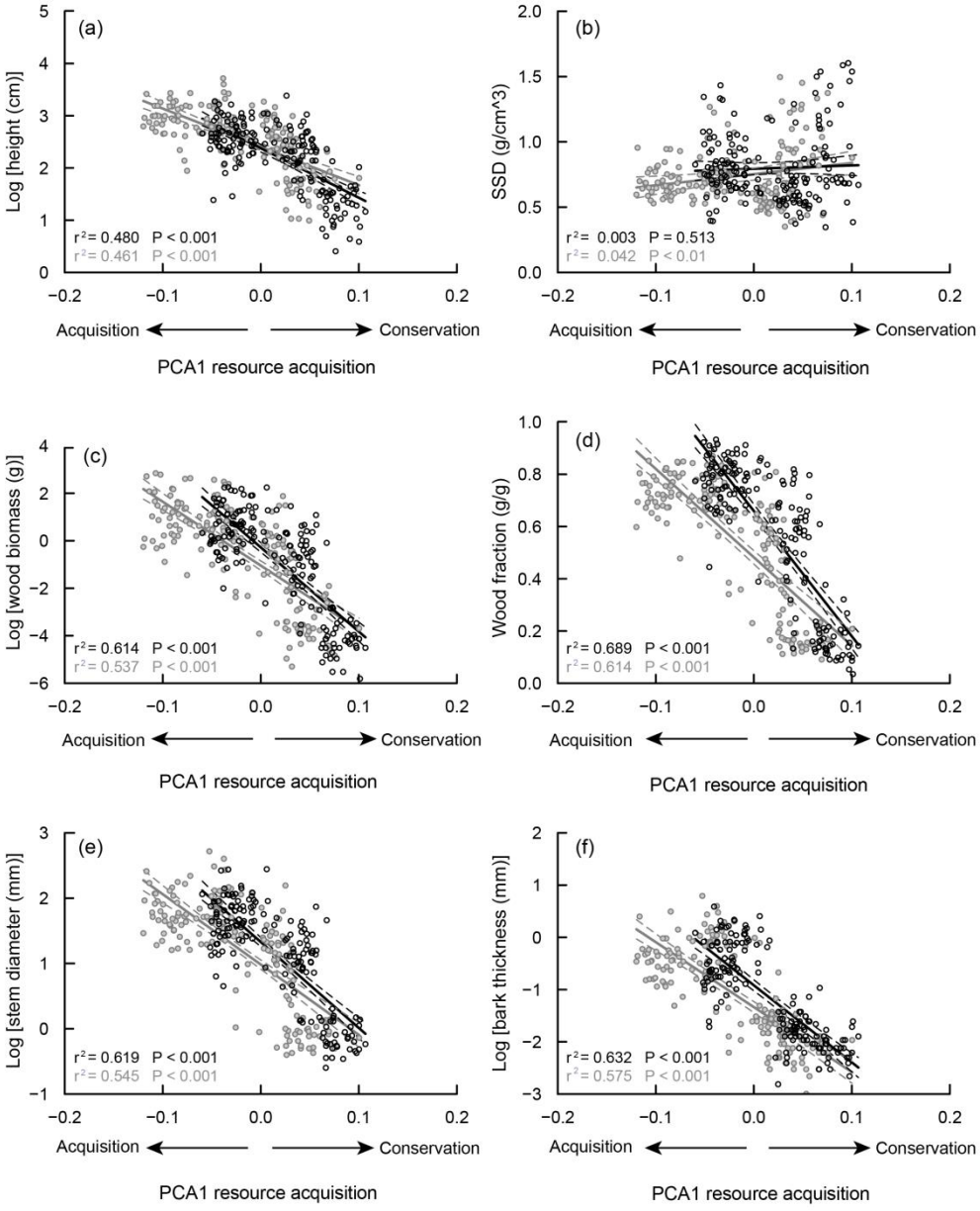

Figure 4.3: Relationships between structural traits (height (a), stem-specific density (b), wood biomass (c), wood fraction (d), total diameter (e), and bark thickness (f)) and the first PC axis of the resource acquisition PCA (leaf economics spectrum). Solid lines are the values predicted by the linear mixed-effect model, dashed lines are the upper and lower limits of the confidence interval of the predicted values, and points are measured data (nutrient addition in grey and no addition in black). Coefficient of correlation (r^2) and significance (P-value) are reported in each panel.

The species with slow return on carbon and nutrient investments (resource conservation), i.e. *L. palustre* and *V. vitis-idaea*, had lower height, thinner stems and bark, less wood biomass, and smaller wood fraction than species with more rapid investment return (faster resource acquisition), i.e. *B. nana* and *S. pulchra* (Fig. 4.3). The relationship between wood fraction and the first axis of the nutrient acquisition strategy PCA changed with fertilization ($F_{1,29} = 19.1$, $P < 0.001$). For height, wood biomass, and stem diameter, relationship changes with fertilization were smaller than for wood fraction, but following the same pattern (Fig. 4.3). In case of bark thickness, the relationship with the first PC axis was the same with and without nutrient addition (parallel). We could not observe a statistically significant relationship between SSD and the first PC axis.

4.4 Discussion

We tested the effects of increased soil temperature and nutrient availability on growth, biomass, and traits of four tundra shrub species. Our findings show that the shrubs grew faster and produced more biomass with enhanced nutrient availability and, in case of biomass, also responded to soil warming, though to a lesser extent. In addition, plant traits showed a coordinated response to fertilization, reflected in the resource acquisition trade-off: shrubs changed from conservation of resources towards more rapid acquisition, as we hypothesised.

4.4.1 Treatment effects on growth, biomass, and plant traits

We expected that soil warming and fertilization treatments would affect plant traits and that the effect would be stronger under combined treatments. However, our results showed that most of the plant traits responded only to nutrient addition and that there was no significant interaction between treatments as shown in other studies (van Wijk *et al.* 2003; DeMarco *et al.* 2014). The lack of interaction between increasing soil temperature and nutrient availability suggests that the treatment effects are additive and that shrub growth, biomass, and traits are soil temperature and nutrient co-limited or limited by the indirect effect of soil temperature on nutrient availability.

The strong trait responses to fertilization might be explained by the large amount of nutrients added to the plots (Giblin *et al.* 1991; Hartley *et al.* 1999; Schaeffer *et al.* 2013). High-latitude ecosystems are highly nutrient-limited and so are plant growth and biomass production (Billings & Mooney 1968; Shaver & Chapin 1980; Epstein *et al.* 2000). Nutrient addition will release

shrubs of this limitation and promote their growth (Chapin & Shaver 1996; DeMarco *et al.* 2014). In addition, the fact that leaf fraction increased with fertilization while the wood fraction decreased, suggests a change of resource allocation towards leaf production.

Plant traits were less responsive to soil warming; only total aboveground and leaf biomass, LA, and LPC responded to soil warming, although more weakly than to fertilization. The smaller trait response to soil warming might be related to the strength of soil warming. Hartley et al. (1999) found effects of soil warming on subarctic shrub growth by using heating cables buried at 5 cm depth, which increased the soil temperature by 5ºC. In our study, however, the heating cables were buried at 15 cm from the surface, deeper than the layer where most of the shrub root biomass occurs (Churchland *et al.* 2010; Wang *et al.* 2016). Thereby, most warming was in the mineral soil layers below 15 cm, whereas the soil temperature increased less than 0.6ºC during the growing season in the root layer. This temperature is lower than the threshold needed for increasing nutrient mineralization (1ºC or greater), limiting the temperature effects to direct ones (Schmidt *et al.* 1999). In addition to the weak soil temperature increase, the short term of the experiment might explain the lack of trait responsiveness to soil warming.

4.4.2 Leaf economics spectrum

Our results showed that species with similar ecological strategies cluster into groups (deciduous and evergreen plant functional types) defined by their leaf traits, which covary tightly in function of the resource acquisition trade-off (Reich *et al.* 1997, 1999). *B. nana* and *S. pulchra* were characterized by leaf traits associated with faster resource acquisition: high SLA and leaf nutrient content, and low LDMC and C:N. In contrast, *L. palustre* and *V. vitis-idaea* were characterized by leaf traits associated with resource conservation. These findings are in line with the evidences of existence of a leaf economics spectrum, which is indicative of species growth strategies (Wright *et al.* 2004; Freschet *et al.* 2010; Díaz *et al.* 2016).

The increase of nutrients promoted a change in the resource acquisition from conservation to faster acquisition, even in the case of the evergreen species. Resource availability is thought to be one of the main drivers of plant strategy selection (Grime 2006; Ordoñez *et al.* 2010). In arctic tundra, where resource availability is low, shrub species adopt a conservative strategy with slow growing and tissue turnover, which enhances plant survival under harsh conditions (Chapin *et al.* 1993). However, the slow traits associated with the conservative strategy are disadvantageous in case of higher resource availability as shrub species could be outcompeted

(e.g., through shading) by other species with faster growth and biomass production (Reich 2014). The rapid tissue turnover of deciduous species might explain the faster adaptation to the new conditions as compared to the evergreen species (Chapin & Shaver 1996).

4.4.3 To grow or to defend

Structural traits of tundra deciduous shrubs are associated with shade-intolerant species. These species invest resources in woody structures to grow taller and faster and to develop wider crowns than the other species in order to outcompete them through light. In contrast, evergreen species (shade-tolerant) grow shorter and slower and produce less biomass (Chapin & Shaver 1996; Cornelissen 1999). Our results suggest that tundra shrubs will promote stronger competition among species with enhanced nutrient availability. Shrubs will grow faster, acquire nutrients more rapidly, and allocate them to produce more leaves at low cost (thin leaves of greater area, higher nutrient content, and lower LDMC and C:N). As a consequence, shrubs will increase their photosynthetic potential and their ability to pre-empt resources, in decrement of their defence (Díaz *et al.* 2016). The expected changes in plant traits driven by nutrient availability enhancement, such as faster growth, greater biomass production, and thinner leaves of greater area, will have a cost for shrubs: lower stress resistance (growth–defence trade-off) (Chapin *et al.* 1993; Chave *et al.* 2009). The faster resource acquisition will make shrubs more vulnerable to herbivory due to higher leaf nitrogen content (Mattson 1980; Díaz *et al.* 2016), to drought because of the water loss associated with bigger leaf surface (Grier & Running 1977), and to adverse environmental conditions (i.e. low nutrient availability) as consequence of low nutrient tissue reserves (Reich 2014). Additionally, our results showed that shrubs grew faster and taller without increasing SSD with nutrient addition, which will enhance shrub vulnerability to pests, mechanical and hydraulic failure, and extreme climatic events (Baraloto *et al.* 2010; Reich 2014; Díaz *et al.* 2016).

4.4.4 Shrub expansion–climate warming feedbacks

Vegetation is strongly coupled with environmental factors (Wookey *et al.,* 2009; Medinski *et al.*, 2010, Iturrate-Garcia *et al.,* 2016). Our results suggest that tundra shrubs will be affected by rising soil temperature projected for the Arctic through indirect effects (e.g. increasing nutrient availability because of accelerated soil organic matter mineralization) and, to a lesser extent, direct effects. The main expected responses will be more rapid resource acquisition and tissue turnover, faster growth strategy, and increased biomass production, in line with previous

experimental studies (Chapin & Shaver 1996; Hudson *et al.* 2011; Elmendorf *et al.* 2012), which will result in shrub expansion (i.e. higher shrub cover) in the short term. However, this faster strategy will increase shrub vulnerability to pests and climate extremes, which are projected to be more frequent (Chapin *et al.* 1993; Francis & Vavrus 2012; IPCC 2013).

Shrub expansion, together with changes in plant strategy and traits, will affect species diversity, surface radiation budget, and ecosystem processes, among others (Chapin *et al.* 1996; Beringer *et al.* 2005). Bryophyte and lichen diversity are expected to decline due to an increase of shrub shading and litter deposition associated with shrub expansion (Cornelissen *et al.* 2001). In turn, permafrost will be affected (Myers-Smith *et al.* 2011); summer permafrost thaw decreases with higher shrub cover (Blok *et al.*, 2010; Nauta *et al.*, 2015), but this protection might be lower than the thermal insulation provided by the cryptogam layer. In addition, the increase of shrub biomass and cover will reduce the canopy albedo and, therefore, increase the net surface radiation (Thompson *et al.* 2004; Beringer *et al.* 2005; Blok *et al.* 2011b). Shrub changes may also affect ecosystem processes, such as higher litter decomposition rate expected with the production of low-cost tissues, which are easier to decompose than the expensive ones.

The climatic conditions projected for the Arctic, the shrub growth sensitivity to climate, and the importance of shrub–climate feedbacks for ecosystem functioning suggest that a special effort should be done to better understand future tundra changes and adaptation to the new climatic conditions. Here, we presented the response of a wide set of traits of some of the dominant species in tussock tundra to soil warming and increased nutrient availability. This response can be considered a step towards more realistic dynamic global vegetation models, although generalization should be considered cautiously due to the short term of the response, which is difficult to extrapolate to the long term (Chapin *et al.* 1995; Boelman *et al.* 2003), the spatial heterogeneity of arctic regions, and the complexity of shrub–climate feedbacks. According to our results, coordinated trait responses representing the whole plant (including ideally wood and root traits) instead of single trait responses are needed for a more robust prediction of shifts in vegetation, climate–vegetation feedbacks, and ecosystem processes.

4.5 Acknowledgement

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4.6 References

See thesis section ‘References’.

CHAPTER 5

General discussion

"Life is really simple,

but we insist on making it complicated"

(*Confucius*)

In order to identify changes in tundra species diversity and plant traits that might take place under climate warming, I explored the relationships between edaphic factors and species diversity and community composition. Furthermore, I investigated responses of shrub growth, aboveground biomass, and traits to experimental soil warming and fertilization. I found interactive effects of plant functional types and edaphic factors on tundra species diversity and community composition (Chapter 2). Moreover, I showed that radial and vertical shrub growth was driven by enhanced nutrient availability, but not by direct effects of soil warming (Chapter 3). Last, I found that, with nutrient addition, shrub species changed their resource acquisition trade-off, from conservative towards more rapid acquisition (Chapter 4). In this final chapter, I will bring these aspects together.

5.1 Arctic tundra diversity and edaphic factors

In tundra ecosystems, soil characteristics are strong predictors of species diversity and community composition (Björk *et al.* 2007; Sundqvist *et al.* 2011). These ecosystems have low species diversity with higher nonvascular than vascular diversity (Billings & Mooney 1968; Gough *et al.* 2000; Sitch *et al.* 2007). Despite the abundance and importance of cryptogams in tundra communities, most studies have focused only on vascular plants (Heikkinen & Neuvonen 1997; Gough *et al.* 2000; Sundqvist *et al.* 2011). Moreover, those studies explored the relationship between species diversity and individual soil variables, although climate change is expected to affect several edaphic factors simultaneously (Gough *et al.* 2000; Chytrý *et al.* 2007). In Chapter 2, I explored the interactive effects between plant functional types (nonvascular and vascular) and soil factors on species diversity and community composition, considering multiple edaphic factors. I found that nonvascular diversity and vascular composition were related to edaphic factors. However, vascular diversity was unrelated, contrary to previous studies showing a strong correlation between species richness and soil variables (Ma 2005; Löbel *et al.* 2006; Gargano *et al.* 2010; Lai *et al.* 2015). Different species physiological tolerance to soil variables might explain the relationship between vascular composition and edaphic factors. Although species composition can vary along edaphic gradients, the number of species could remain the same (i.e. different species, but same number), which would overshadow the relationship between vascular diversity and edaphic factors. Furthermore, opposite trends in response to individual edaphic factors (e.g. species diversity decrease with moisture and increase with soil acidity) might be hidden when considering simultaneously

multiple edaphic factors. These findings suggest that cryptogam diversity might be more vulnerable than vascular diversity to variation of edaphic factors associated with climate change.

5.2 Shrub growth in a warmer Arctic

Tundra shrub growth is suggested to be co-limited by low air temperature and nutrient availability (Billings & Mooney 1968; Shaver & Chapin 1980; Epstein *et al.* 2000). Although faster growth is expected with increasing air temperature, shrub growth sensitivity to climate remains uncertain (Myers-Smith *et al.* 2015a). To better understand the drivers of shrub growth, I explored growth rate responses to two abiotic factors associated to climate warming (i.e. soil temperature and nutrient availability) by combining experimental manipulation of the suggested drivers with dendroecology (Chapter 3). The study species grew faster – radially and vertically – with nutrient addition, but not with soil warming, suggesting that shrub growth was mainly limited by nutrient availability. These findings are contrary to previous dendrochronological studies in the area, which showed strong correlation between shrub growth and summer air temperature (Blok *et al.* 2011a; Li *et al.* 2016). The contradictory responses might be explained by the short duration of the soil warming and fertilization experiment (Chapters 3 and 4), weak strength of the soil warming (< 0.6°C in the root layer during the growing season), statistical analysis using linear mixed-effect models instead of correlations, and different shrub responses to air and soil temperature (Chapin *et al.* 1995; Weih & Karlsson 2001; Boelman *et al.* 2003; Lapointe-Garant *et al.* 2010; Myers-Smith *et al.* 2015a). Moreover, the positive correlation between shrub growth and air temperature found in the dendrochronological studies (Blok *et al.* 2011a; Li *et al.* 2016) might be explained by indirect effects of air temperature, such as permafrost thawing and faster soil organic matter mineralization, which will enhance nutrient availability (Schmidt, Jonasson & Michelsen 1999; Weih & Karlsson 2001; Walther *et al.* 2002; Schuur *et al.* 2009). These indirect effects are difficult to identify in dendrochronological studies, because only temporal series of air temperature are used, but not series of soil temperature, active layer thickness or soil nutrient concentrations. However, experimental dendroecological approaches, like the one I used (Chapter 3), can allow us to separate direct from indirect effects by manipulating specific growth drivers.

5.3 Coordinated trait responses of shrubs – to grow or to defend

Plant strategies are defined by the way plants use resources (nutrients, water, and light) to grow, reproduce, compete with neighbour plants, and defend themselves against pathogens and herbivores (Bazzaz *et al.* 1987; Ordoñez *et al.* 2010). However, as resources are limited in tundra ecosystems, plants are unable to perform well in all these function simultaneously (trade-off) (Grime 1977; Westoby *et al.* 2002; Reich 2014). Tundra plant adaptation to harsh environmental conditions is reflected in their conservative strategies and plant traits (Shaver & Chapin 1980; Reich, Walters & Ellsworth 1997; Cornelissen 1999). In Chapter 4, I hypothesised that tundra shrubs will change their growth strategy and resource acquisition trade-off from slow towards more rapid ones with direct and indirect effects of climate warming, and that plant trait will respond in a coordinate way to the treatments. While I indeed found the expected responses, these responses were driven by nutrient addition and not by soil warming, suggesting that indirect effects of climate warming on plant strategy and trade-off selection might be more important than direct effects. The faster shrub growth strategy and more rapid resource acquisition shown in Chapter 4, together with denser canopies, might result in shrub expansion in the short term. However, the resource allocation to growth may compromise shrub defence (Grime 1977; Chapin, Autumn & Pugnaire 1993). In line with this growth–defence trade-off, I found thinner bark, lower bark investment, and a coordinated leaf trait response towards "low-cost" tissues and rapid nutrient turnover with fertilization (Chapters 3 and 4). Thereby, shrubs may become more vulnerable to mechanical failure, herbivory, pathogens, and climate extremes (e.g. frost and drought events) in the long term due to indirect effects (Kozlowski 1992; Rowe & Speck 2005; Paine *et al.* 2010; Lens *et al.* 2011).

5.4 Implications and future research

Findings of my work highlight the need of incorporating several aspects in studies exploring the effects of climate change on species diversity, distribution, and plant traits, especially in tundra ecosystems. One important aspect is to consider tundra cryptogams species in diversity studies, due to their abundance and important role in different processes such as shaping vascular diversity and protecting permafrost from thawing. Additionally, to identify climate change effects on species diversity, relationships between species diversity and multiple edaphic factors should be considered, as climate change may affect several soil variables simultaneously.

Similarly, coordinated trait responses to environmental changes need to be included in studies investigating climate change effects on plant traits. Finally, due to the complexity of mechanisms driving shifts in species diversity, distribution, and plant traits, I suggest to combine different methodological approaches to identify those mechanisms. All these aspects may contribute to more realistic dynamic global vegetation models and, therefore, to robust predictions of species composition and diversity shifts in a warming climate.

Identifying potential effects of climate change on tundra vegetation, as done in this study, is a first step to investigate tundra vegetation–climate feedbacks in a changing Arctic. However, to complete our knowledge of tundra vegetation responses to climate change, future research needs to extend the study species and locations due to species- and plant functional type-specific responses to environmental factors and to the high spatial heterogeneity of the Arctic (Walker 2000; Lantz *et al.* 2010; Mod *et al.* 2014; Iturrate-Garcia *et al.* 2016). Furthermore, due to the close relation between edaphic factors and vegetation in tundra ecosystems, future efforts should focus on investigating how atmospheric changes will propagate into edaphic factors for more reliable predictions of vegetation shifts with climate change (Seneviratne *et al.* 2010; Walwoord & Kurylyk 2016). In addition, running new experiments simulating different climate scenarios projected for the Arctic (e.g. precipitation and cloud cover increase, snow cover decrease (IPCC, 2013)) and manipulating edaphic factors according to expected atmospheric propagation will reduce uncertainties of vegetation responses to climate.

Vegetation responses to climate change will alter the surface radiation budget and the carbon and water cycle, which will affect in turn climate. While processes like carbon cycling have extensively been studied in tundra ecosystems, effects of species diversity shifts on the surface radiation budget are still uncertain in terms of direction and magnitude (e.g., Shaver & Chapin 1991; Oechel *et al.* 1993; Epstein *et al.* 2012; Forkel *et al.* 2016; Webb *et al.* 2016). Future research should focus on the surface radiation budget to better understand vegetation–climate feedbacks. For that, I propose the use of three-dimensional radiative transfer models to study the surface radiation budget of tundra vegetation, including spectral reflectance of the canopy and transmitted radiation. These physical models can be used to describe the interaction of light with the vegetation canopy and its background, including multiple scattering and mutual shading (Kötz *et al.* 2004; Jacquemoud *et al.* 2009; Niemann *et al.* 2012; Schneider *et al.* 2014). Three-dimensional objects mimicking plant species can be included in these models (e.g. DART model) (Gastellu-Etchegorry *et al.* 1996; Juszak *et al.* 2014). Therefore, these models will allow

us to run diversity experiments (i.e. *in silico* experiments) modifying number, composition, and abundance of species, but also experiments varying plant traits. Datasets similar to the one included in this study can be used as input data for more realistic simulations. These *in silico* experiments will provide insight into the effects that species diversity, community composition, and plant traits may have on the surface radiation budget, permafrost (e.g. thawing protection by shading or thermal insulation) and, therefore, on regional climate.

5.5 Conclusions

The climatic conditions projected for the Arctic, species diversity vulnerability to climate change, and importance of tundra vegetation–climate feedbacks for ecosystem functioning suggest that a special effort should be done to better understand tundra vegetation shifts and adaptation to future climatic conditions (Chapin & Shaver 1996; Cornelissen *et al.* 2001; Beringer *et al.* 2005; Chapin *et al.* 2005; IPCC 2013). Although shifts and adaptation have been intensively studied for selected locations and species, different responses are expected because of the high spatial heterogeneity across the Arctic and species-specific responses to climate (Walker 2000; Lantz *et al.* 2010). In this study, I found that species diversity and community composition were closely related to edaphic factors and that those relationships were different between plant functional types (i.e. nonvascular and vascular) (Chapter 2). Moreover, I showed shrub growth sensitivity to indirect effects of climate warming, i.e. enhanced nutrient availability (Chapter 3), and coordinated response of shrub traits to these effects (Chapter 4), suggesting a shift in growth strategy and resource acquisition trade-off towards more rapid ones. This thesis therefore contributes towards an increased knowledge of tundra diversity vulnerability and plant trait shifts in a changing Arctic, especially in northeastern Siberia, where there are large gaps of information (Elmendorf *et al.* 2012; Walker *et al.* 2013). Furthermore, the planned use of these data for further research using 3D radiative transfer modelling, will improve our understanding of species diversity and trait effects on the surface radiation budget in tundra ecosystems. Such an understanding is essential for reducing the uncertainties in direction and magnitude of tundra vegetation–climate feedbacks.

5.6 References

See thesis section ‘References’.

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Appendix 1: Description of the observational plots

This appendix includes the description of the observational plots used in Chapter 2 (Table A1.1). Definition of some of the terms used to describe the plots can be found below.

Moisture class

- Dry: the top 2 cm of the soil is dry to the touch during the warmest month of the year.
- Moisture: soils are moist year round, but standing water is not present.
- Wet: standing water is found during the warmest month of the year.

ALT: maximum active layer thickness measured on 14th August 2014.

Dominant vegetation

- Graminoid[1]: *Eriophorum angustifolium*.
- Graminoid[2]: *Eriophorum vaginatum*.
- Moss[1]: *Sphagnum* spp.

LF: landscape features

- LF1: *Betula nana* polygon in polygonal tundra.
- LF2: clearing in *B. nana* polygon in polygonal tundra.
- LF3: transition between wet hollow and *B. nana* polygon in polygonal tundra.
- LF4: transition between wet hollow and *B. nana* polygon in tussock tundra.
- LF5: tussock tundra.
- LF6: wet hollow in polygonal tundra.
- LF7: wet hollow in tussock tundra.

CAVM: circumpolar arctic vegetation map vegetation types (see also Chapter 1)

- G4: tussock sedge, dwarf shrub, moss tundra.
- P2: prostrate/hemiprostrate dwarf shrub tundra.
- S1: erect dwarf shrub tundra.
- S1.2: dwarf shrub, lichen tundra.
- W2: sedge, moss, dwarf shrub wetland.

Table A1.1: Description of the observational plots used in Chapter 2.

Plot	Location	Latitude (N)	Longitude (E)	Elevation (m)	Moisture class	ALT (cm)	Dominant vegetation	Mean canopy height (cm)	LF	CAVM
01	Ridge	70.8268	147.4636	27.3	dry	45.0	moss/lichen	6.9	LF4	G4
02	Ridge	70.8261	147.4627	26.7	moist	44.5	moss	8.1	LF5	S1
03	Ridge	70.8259	147.4631	26.6	moist	61.0	moss/shrub	6.5	LF5	S1.2
04	Ridge	70.8279	147.4588	27.7	moist	69.0	moss/graminoid[2]	10.0	LF5	G4
05	Ridge	70.8265	147.4628	26.8	dry	30.0	moss	7.0	LF5	S1
06	Ridge	70.8274	147.4617	25.8	moist	43.0	moss	9.3	LF5	S1
07	Ridge	70.8264	147.4648	25.6	wet	54.0	graminoid[1]	25.8	LF7	W2
08	Ridge	70.8282	147.4635	26.0	moist	58.0	moss/graminoid[2]	9.3	LF5	G4
09	Ridge	70.8281	147.4642	25.8	moist	56.0	graminoid[2]	9.7	LF5	G4
10	Ridge	70.8275	147.4658	25.5	moist	53.0	moss	10.2	LF5	G4
11	Ridge	70.8290	147.4645	25.4	dry	56.0	moss	4.5	LF5	S1.2
12	Ridge	70.8296	147.4645	24.8	moist	46.0	moss	9.8	LF5	G4
13	Ridge	70.8294	147.4649	13.8	moist	56.0	moss	8.5	LF5	G4
14	Ridge	70.8279	147.4693	14.4	dry	45.0	moss/lichen	8.2	LF5	S1.2
15	Ridge	70.8289	147.4519	15.8	dry	56.0	moss/shrub	10.6	LF5	P2
16	Lakebed	70.8317	147.4909	7.2	wet	65.0	graminoid[1]	36.7	LF6	W2
17	Lakebed	70.8317	147.4925	8.3	dry	33.0	moss/lichen	6.0	LF1	S1
18	Lakebed	70.8317	147.4936	8.6	moist	50.0	moss[1]	17.7	LF7	W2
19	Lakebed	70.8327	147.4943	8.9	dry	24.0	moss/shrub	16.7	LF1	S1
20	Lakebed	70.8327	147.4977	9.2	dry	43.0	moss/shrub	12.5	LF1	S1
21	Lakebed	70.8331	147.4902	9.8	dry	33.0	moss	10.8	LF3	S1
22	Lakebed	70.8334	147.4916	10.3	dry	35.0	moss/lichen	11.4	LF1	S1
23	Lakebed	70.8334	147.4926	10.3	moist	60.0	moss[1]	25.4	LF7	W2
24	Lakebed	70.8334	147.4977	9.2	moist	31.0	moss/lichen	6.6	LF3	S1.2
25	Lakebed	70.8345	147.4910	9.4	dry	39.0	moss/shrub	19.3	LF1	S1
26	Lakebed	70.8348	147.4926	9.5	dry	30.0	moss/shrub	19.6	LF1	S1
27	Lakebed	70.8348	147.4967	9.7	moist	44.0	moss/lichen	7.5	LF3	S1.2
28	Lakebed	70.8343	147.4916	9.8	moist	54.0	moss[1]/graminoid[1]	17.8	LF6	W2
29	Lakebed	70.8343	147.4967	10.0	moist	53.0	moss[1]/graminoid[1]	10.5	LF6	W2
30	Lakebed	70.8356	147.4950	10.2	moist	50.0	moss[1]	21.6	LF3	G4/S1
31	Ridge	70.8265	147.4639	26.0	wet	58.0	graminoid[2]	38.3	LF7	W2
32	Ridge	70.8259	147.4624	25.9	moist	57.0	moss	5.0	LF5	S1.2
33	Ridge	70.8278	147.4592	30.2	moist	62.0	graminoid[2]	17.4	LF5	G4
34	Ridge	70.8286	147.4630	27.9	moist	55.0	moss/graminoid[2]	14.5	LF5	S1
35	Ridge	70.8286	147.4694	30.5	dry	55.0	graminoid[2]	8.9	LF5	P2
36	Lakebed	70.8327	147.4954	9.1	dry	46.0	lichen	6.4	LF1	S1.2
37	Lakebed	70.8344	147.4964	11.8	moist	36.5	moss[1]	12.7	LF3	W2
38	Lakebed	70.8353	147.4935	11.1	moist	28.0	moss	7.5	LF2	S1.2
39	Lakebed	70.8347	147.4907	10.5	moist	26.0	moss/shrub	9.1	LF3	S1
40	Lakebed	70.8329	147.4909	10.4	moist	32.0	moss/shrub	8.8	LF3	S1

Appendix 2: Species composition list

Species composition and abundance of the observational plots used in Chapter 2 are shown in this appendix (Tables A2.1a, A2.1b, A2.2a, A2.2b). A plot-size grid (0.5 × 0.5 m) divided into 25 quadrats of 0.1 × 0.1 m was used to assess the species composition and abundance in each plot (Fig. A2.1).

All the species in each quadrat were identified in order to calculate the species richness of each plot, which was the sum of number of species in every grid quadrat. Additionally, species presence/absence in every quadrat was noted down to estimate species abundance. For that, the number of quadrats where a species was present was divided by the total number of grid quadrats (twenty-five).

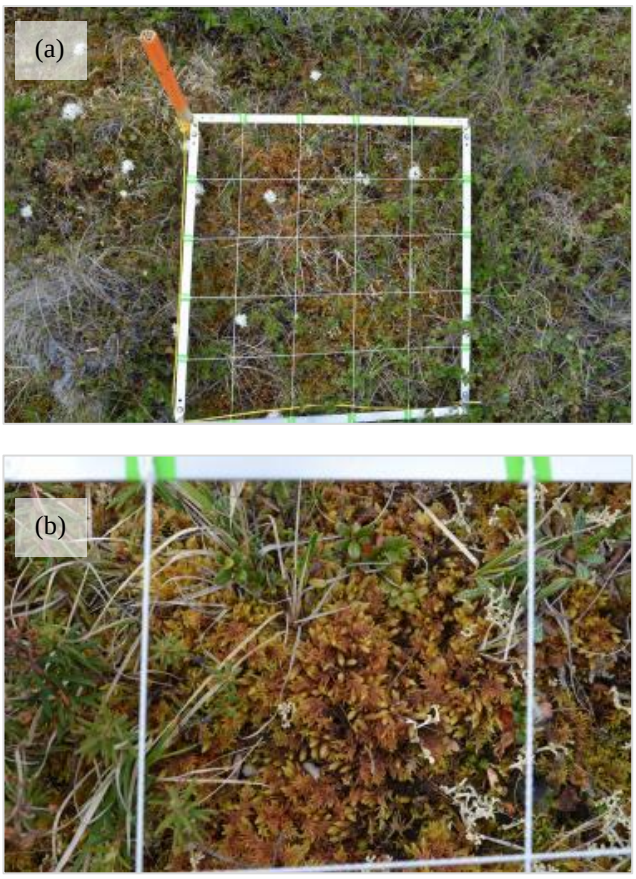

Figure A2.1: Sampling grid for the diversity assessment (a); detail of one grid quadrat (b).

Table A2.1a: Species name including authority, abbreviation, and abundance on the ridge plots (P01-10).

Species name	Abbr.	01	02	03	04	05	06	07	08	09	10
Shrubs											
Arctous alpina (L.) Nied.	Arctalpi	0	0	25	0	0	0	0	0	0	0
Betula nana ssp. *exilis* (Sukazcev) Hultén	Betunana	8	16	1	15	22	15	9	13	16	18
Cassiope tetragona (L.) D. Don.	Casstetr	0	0	0	0	0	0	0	0	0	0
Dryas octopetala L.	Dryaocto	0	3	12	0	0	0	0	0	0	0
Ledum palustre ssp. *decumbens* (Aiton) Hultén	Ledupalu	21	20	19	22	22	23	0	19	24	18
Salix fuscenses Andersson	Salifusc	0	0	0	0	0	0	0	0	0	0
Salix glauca L.	Saliglau	0	0	0	0	0	0	0	0	0	0
Salix pulchra Cham.	Salipulc	0	1	0	3	6	2	11	3	0	2
Vaccinium uliginosum L.	Vacculig	0	8	0	12	0	0	0	1	0	0
Vaccinium vitis-idaea L.	Vaccviti	24	25	25	25	25	25	0	23	25	25
Forbs											
Petasites frigidus (L.) Fr.	Petafrig	0	0	0	0	0	0	0	0	1	0
Parrya nudicaulis (L.) Boiss.	Parrnudi	1	0	0	0	0	0	0	0	0	0
Pedicularis capitata Adams	Pedicapi	0	0	0	0	0	0	0	0	0	0
Pedicularis lapponica L.	Pedilapp	0	0	0	0	0	0	0	0	0	0
Pyrola grandiflora Radius	Pyrogran	0	3	0	0	0	0	0	0	0	0
Saxifraga nelsoniana D. Don	Saxinels	0	0	0	0	0	0	0	0	3	0
Valeriana capitata Pall. ex Link	Valecapi	3	2	0	0	1	0	0	0	0	0
Graminoids											
Arctagrostis latifolia (R.Br.) Griseb.	Arctlati	12	2	0	2	11	6	0	0	0	0
Calamagrostis holmii Lange	Calaholm	0	9	16	15	16	20	0	9	11	6
Carex aquatilis var. *minor* Boott	Careaqua	0	0	0	0	0	0	0	0	0	6
Carex bigelowii ssp. *arctisibirica* (Jurtzev) Á.& D.Löve	Carebige	0	22	21	0	8	3	0	9	0	0
Eriophorum angustifolium Honck.	Erioangu	0	0	0	0	0	0	25	0	0	0
Eriophorum vaginatum L.	Eriovagi	9	0	0	12	2	1	0	23	22	19
Luzula nivalis (Laest.) Spreng.	Luzuniva	1	0	0	0	0	0	0	0	0	0
Luzula wahlenbergii Rupr.	Luzuwahl	0	0	0	0	0	0	0	0	0	0
Bryophytes											
Aulacomnium palustre (Hedw.) Schwägr.	Aulapalu	0	0	24	12	8	24	11	11	24	12
Aulacomnium turgidum (Wahlenb.) Schwägr.	Aulaturg	0	22	8	0	2	0	0	0	0	8
Blepharostoma trichophyllum (L.) Dumort.	Bleptric	0	0	0	0	0	0	0	0	0	0
Brachythecium sp.	Bracsp	0	0	0	0	0	0	0	0	0	0
Dicranum elongatum Schleich. ex Schwägr.	Dicrelon	20	4	6	17	15	0	0	23	12	0
Dicranum spadiceum J.E. Zetterst	Dicrspad	20	4	0	0	15	23	0	0	12	25
Dicranum sp.	Dicrsp	0	0	0	0	0	0	0	0	0	0
Hylocomium splendens (Hedw.) Schimp.	Hylosple	4	25	13	23	10	18	0	0	15	5
Polytrichastrum alpinum (Hedw.) G.L. Sm.	Polyalpi	0	8	0	0	0	0	0	0	0	0
Polytrichum hyperboreum R. Br.	Polyhype	1	0	0	0	0	0	0	0	0	0
Polytrichum jensenii I. Hagen	Polyjens	0	0	0	0	0	0	0	7	0	3
Polytrichum juniperinum Hedw.	Polyjuni	0	0	17	7	3	0	0	0	3	0
Polytrichum piliferum Hedw.	Polypili	0	0	0	0	0	0	0	11	0	0

(continuation)

Species name	Abbr.	01	02	03	04	05	06	07	08	09	10
Bryophytes											
Ptilidium ciliare (L.) Hampe	Ptilcili	0	2	5	0	21	0	0	0	0	7
Sanionia uncinata (Hedw.) Loeske	Saniunci	0	0	0	0	0	0	0	0	0	0
Sphagnum balticum (Russow) C.E.O. Jensen	Sphabalt	0	0	0	0	0	0	0	9	0	0
Sphagnum compactum Lam. & DC.	Sphacomp	0	0	0	0	0	0	0	0	0	0
Sphagnum lenense Pohle	Sphalene	0	0	0	0	0	0	0	0	0	1
Sphagnum obtusum Warnst.	Sphaobtu	0	0	0	0	0	0	19	0	0	0
Sphagnum squarrosum Crome	Sphasqua	0	0	0	0	0	0	0	0	0	0
Sphagnum teres (Schimp.) Ångström	Sphatere	0	0	0	0	0	0	0	23	0	0
Sphenolobus minutus (Schreb.) Berggr.	Spheminu	20	4	6	20	15	23	0	14	12	25
Tomentypnum nitens (Hedw.) Loeske	Tomenite	21	0	18	1	24	18	3	0	2	12
Tritomaria exsectiformis (Breidl.) Schiffner ex Loeske	Tritexse	0	0	0	0	0	0	0	0	0	0
Lichens											
Alectoria nigricans (Ach.) Nyl	Alecnigr	0	0	0	0	0	0	0	0	0	0
Cetraria ericetorum Opiz	Cetreric	0	0	0	16	0	0	0	0	0	0
Cetraria islandica (L.) Ach.	Cetrisla	20	7	22	8	0	10	0	0	5	0
Cladonia amaurocraea (Florke) Schaerer	Cladamau	0	0	0	2	0	0	0	0	0	0
Cladonia borealis S. Stenroos	Cladbore	0	0	0	0	0	0	0	0	0	0
Cladonia cenotea (Ach.) Schaerer	Cladceno	0	0	0	0	0	0	0	0	0	0
Cladonia chlorophaea (Florke ex Sommerf.) Sprengel	Cladchlo	0	0	0	0	0	0	0	0	0	0
Cladonia coccifera (L.) Willd.	Cladcocc	0	0	2	5	0	0	0	0	0	0
Cladonia cornuta (L.) Hoffm.	Cladcorn	0	0	0	0	0	0	0	0	0	0
Cladonia cyanipes (Sommerf.) Nyl.	Cladcyan	0	0	0	0	0	0	0	0	0	0
Cladonia deformis (L.) Hoffm.	Claddefo	0	0	0	0	0	0	0	0	0	0
Cladonia ecmocyna Leighton	Cladecmo	0	0	0	0	0	0	0	0	0	0
Cladonia gracilis (L.) Willd.	Cladgrac	0	4	4	0	0	0	0	0	0	0
Cladonia macroceras (Delise) Hav.	Cladmacr	0	0	0	1	0	0	0	0	0	0
Cladonia pleurota (Florke) Schaerer	Cladpleu	0	0	0	0	0	0	0	0	0	0
Cladonia rangiferina (L.) F. H. Wigg.	Cladrang	13	0	0	0	0	0	0	0	0	0
Cladonia sulphurina (Michaux) Fr.	Cladsulp	0	0	0	0	0	0	0	0	0	0
Dactylina arctica (Richardson) Nyl.	Dactarct	18	0	15	2	0	0	0	13	0	0
Flavocetraria cucullata (Bellardi) Karnefelt & Thell	Flavcucu	24	16	23	0	0	8	0	0	17	2
*Nephroma expallidum (*Nyl.) Nyl.	Nephexpa	0	0	0	0	0	0	0	0	0	0
Ochrolechia inaequatula (Nyl.) Zahlbr.	Ochrinae	0	3	0	0	3	0	0	0	0	0
Peltigera aphtosa (L.) Willd.	Peltapht	9	0	13	0	16	0	0	0	0	0
Peltigera frippii Holt.-Hartw.	Peltfrip	0	0	2	4	1	0	0	0	0	0
Peltigera leucophlebia (Nyl.) Gyelnik	Peltleuc	0	19	0	15	0	0	0	0	0	12
Peltigera occidentalis (Å.E. Dahl) Kristinsson	Peltocci	0	0	0	0	0	0	0	1	0	0
Peltigera scabrosa Th. Fr.	Peltscab	8	0	0	0	5	8	0	2	9	0
Protopannaria pezizoides (Weber) Joerg & Ekman	Protpezi	0	0	0	0	0	0	0	0	0	0
Stereocaulon alpinum Laurer ex Funck	Steralpi	0	0	1	0	0	0	0	0	0	0
Thamnolia vermicularis (Sw.) Ach. ex Schaerer	Thamverm	0	0	3	0	0	0	0	0	0	0

Table A2.1b: Species name including authority, abbreviation, and abundance on the ridge plots (P11-15, P31-35).

Species name	Abbr.	11	12	13	14	15	31	32	33	34	35
Shrubs											
Arctous alpina (L.) Nied.	Arctalpi	0	0	0	0	0	0	18	0	0	0
Betula nana ssp. *exilis* (Sukazcev) Hultén	Betunana	1	16	15	2	5	14	7	18	16	14
Cassiope tetragona (L.) D. Don.	Casstetr	0	2	0	0	20	0	0	0	0	17
Dryas octopetala L.	Dryaocto	3	1	0	0	3	0	3	0	0	0
Ledum palustre ssp. *decumbens* (Aiton) Hultén	Ledupalu	20	25	19	25	23	0	23	19	16	20
Salix fuscenses Andersson	Salifusc	0	0	0	0	0	0	0	0	0	0
Salix glauca L.	Saliglau	1	0	0	0	0	0	0	0	0	0
Salix pulchra Cham.	Salipulc	0	4	1	1	0	15	0	7	3	0
Vaccinium uliginosum L.	Vacculig	10	0	0	0	0	3	1	0	18	0
Vaccinium vitis-idaea L.	Vaccviti	25	25	24	25	25	0	25	22	0	25
Forbs											
Petasites frigidus (L.) Fr.	Petafrig	0	0	0	0	0	0	0	0	0	0
Parrya nudicaulis (L.) Boiss.	Parrnudi	0	0	0	0	0	0	1	0	0	0
Pedicularis capitata Adams	Pedicapi	0	0	0	0	0	0	1	0	0	0
Pedicularis lapponica L.	Pedilapp	0	0	5	0	0	0	0	0	0	0
Pyrola grandiflora Radius	Pyrogran	0	0	0	0	0	0	0	0	0	0
Saxifraga nelsoniana D. Don	Saxinels	0	0	0	1	2	0	2	0	0	0
Valeriana capitata Pall. ex Link	Valecapi	1	1	0	0	2	0	5	0	0	0
Graminoids											
Arctagrostis latifolia (R.Br.) Griseb.	Arctlati	0	0	0	0	0	0	1	3	4	3
Calamagrostis holmii Lange	Calaholm	1	10	9	7	16	0	5	0	6	5
Carex aquatilis var. *minor* Boott	Careaqua	0	0	0	0	0	0	0	0	0	4
Carex bigelowii ssp. *arctisibirica* (Jurtzev) Á.& D.Löve	Carebige	20	2	9	10	12	0	21	0	0	0
Eriophorum angustifolium Honck.	Erioangu	0	0	0	0	0	25	0	0	0	0
Eriophorum vaginatum L.	Eriovagi	3	10	10	13	5	0	0	25	17	20
Luzula nivalis (Laest.) Spreng.	Luzuniva	0	0	0	0	0	0	0	0	0	0
Luzula wahlenbergii Rupr.	Luzuwahl	0	0	0	0	0	0	0	0	0	0
Bryophytes											
Aulacomnium palustre (Hedw.) Schwägr.	Aulapalu	2	16	3	7	4	0	10	10	6	12
Aulacomnium turgidum (Wahlenb.) Schwägr.	Aulaturg	0	16	0	23	3	0	2	0	0	0
Blepharostoma trichophyllum (L.) Dumort.	Bleptric	0	0	0	0	0	0	0	0	0	0
Brachythecium sp.	Bracsp	0	0	0	0	0	0	0	0	1	0
Dicranum elongatum Schleich. ex Schwägr.	Dicrelon	16	15	20	25	20	0	0	0	0	0
Dicranum spadiceum J.E. Zetterst	Dicrspad	16	15	20	0	0	0	0	0	0	0
Dicranum sp.	Dicrsp	0	0	0	0	0	0	7	0	0	12
Hylocomium splendens (Hedw.) Schimp.	Hylosple	23	22	9	0	3	0	0	10	0	8
Polytrichastrum alpinum (Hedw.) G.L. Sm.	Polyalpi	0	0	0	0	0	0	0	0	0	0
Polytrichum hyperboreum R. Br.	Polyhype	0	0	0	0	9	0	0	0	0	0
Polytrichum jensenii I. Hagen	Polyjens	0	0	0	0	0	0	0	0	0	0
Polytrichum juniperinum Hedw.	Polyjuni	3	0	2	2	0	0	16	0	0	0
Polytrichum piliferum Hedw.	Polypili	0	0	0	0	0	0	0	0	0	0

(continuation)

Species name	Abbr.	11	12	13	14	15	31	32	33	34	35
Bryophytes											
Ptilidium ciliare (L.) Hampe	Ptilcili	0	10	5	0	0	0	0	0	14	2
Sanionia uncinata (Hedw.) Loeske	Saniunci	1	0	0	0	0	0	0	0	0	0
Sphagnum balticum (Russow) C.E.O. Jensen	Sphabalt	0	0	0	0	0	0	0	0	0	0
Sphagnum compactum Lam. & DC.	Sphacomp	0	0	0	0	0	0	0	5	15	0
Sphagnum lenense Pohle	Sphalene	0	0	0	0	0	0	0	0	0	0
Sphagnum obtusum Warnst.	Sphaobtu	0	0	0	0	0	0	0	0	0	0
Sphagnum squarrosum Crome	Sphasqua	0	0	0	0	0	4	0	0	0	0
Sphagnum teres (Schimp.) Ångström	Sphatere	0	0	0	0	0	0	0	0	0	0
Sphenolobus minutus (Schreb.) Berggr.	Spheminu	16	15	20	25	20	0	7	0	0	12
Tomentypnum nitens (Hedw.) Loeske	Tomenite	22	9	10	0	23	0	7	12	18	16
Tritomaria exsectiformis (Breidl.) Schiffner ex Loeske	Tritexse	0	0	0	0	0	0	0	0	0	0
Lichens											
Alectoria nigricans (Ach.) Nyl	Alecnigr	0	0	0	0	0	0	5	0	0	0
Cetraria ericetorum Opiz	Cetreric	0	0	0	0	0	0	0	0	0	0
Cetraria islandica (L.) Ach.	Cetrisla	22	8	10	24	19	0	17	0	0	7
Cladonia amaurocraea (Florke) Schaerer	Cladamau	0	0	0	0	0	0	0	0	0	0
Cladonia borealis S. Stenroos	Cladbore	0	2	0	0	0	0	0	0	0	0
Cladonia cenotea (Ach.) Schaerer	Cladceno	0	0	0	0	0	0	0	0	0	0
Cladonia chlorophaea (Florke ex Sommerf.) Sprengel	Cladchlo	4	0	0	0	0	0	0	0	0	0
Cladonia coccifera (L.) Willd.	Cladcocc	5	0	0	0	0	0	5	0	0	0
Cladonia cornuta (L.) Hoffm.	Cladcorn	0	0	0	0	0	0	1	0	0	0
Cladonia cyanipes (Sommerf.) Nyl.	Cladcyan	0	0	0	0	0	0	2	0	0	5
Cladonia deformis (L.) Hoffm.	Claddefo	0	0	0	0	0	0	0	0	0	0
Cladonia ecmocyna Leighton	Cladecmo	0	0	1	0	0	0	0	0	0	0
Cladonia gracilis (L.) Willd.	Cladgrac	0	0	0	0	3	0	12	0	0	6
Cladonia macroceras (Delise) Hav.	Cladmacr	0	0	1	0	0	0	0	0	0	0
Cladonia pleurota (Florke) Schaerer	Cladpleu	0	0	0	0	0	0	0	0	0	0
Cladonia rangiferina (L.) F. H. Wigg.	Cladrang	0	0	0	0	0	0	0	0	0	0
Cladonia sulphurina (Michaux) Fr.	Cladsulp	1	0	0	0	0	0	0	0	0	0
Dactylina arctica (Richardson) Nyl.	Dactarct	4	0	0	0	1	0	20	0	0	7
Flavocetraria cucullata (Bellardi) Karnefelt & Thell	Flavcucu	25	21	17	25	25	0	23	25	0	3
*Nephroma expallidum (*Nyl.) Nyl.	Nephexpa	0	3	0	0	0	0	0	0	0	0
Ochrolechia inaequatula (Nyl.) Zahlbr.	Ochrinae	0	0	3	0	4	0	5	0	0	7
Peltigera aphtosa (L.) Willd.	Peltapht	16	7	7	2	17	0	9	10	4	16
Peltigera frippii Holt.-Hartw.	Peltfrip	7	0	0	0	0	0	0	0	0	0
Peltigera leucophlebia (Nyl.) Gyelnik	Peltleuc	0	0	0	0	2	0	0	0	8	0
Peltigera occidentalis (Å.E. Dahl) Kristinsson	Peltocci	0	0	0	0	0	0	0	0	0	0
Peltigera scabrosa Th. Fr.	Peltscab	0	0	3	0	0	0	0	0	0	0
Protopannaria pezizoides (Weber) Joerg & Ekman	Protpezi	0	0	0	0	0	0	0	0	0	0
Stereocaulon alpinum Laurer ex Funck	Steralpi	0	0	0	0	0	0	0	0	0	0
Thamnolia vermicularis (Sw.) Ach. ex Schaerer	Thamverm	0	0	0	0	0	0	2	0	0	0

Table A2.2a: Species name including authority, abbreviation, and abundance on the lakebed plots (P16-25).

Species name	Abbr.	16	17	18	19	20	21	22	23	24	25
Shrubs											
Arctous alpina (L.) Nied.	Arctalpi	0	0	0	0	0	0	0	0	0	0
Betula nana ssp. *exilis* (Sukazcev) Hultén	Betunana	0	22	3	24	20	22	22	0	11	12
Cassiope tetragona (L.) D. Don.	Casstetr	0	0	0	0	0	0	0	0	0	0
Dryas octopetala L.	Dryaocto	0	0	0	0	0	0	0	0	0	0
Ledum palustre ssp. *decumbens* (Aiton) Hultén	Ledupalu	0	0	0	0	0	0	0	0	0	0
Salix fuscenses Andersson	Salifusc	0	0	0	0	0	0	0	0	0	0
Salix glauca L.	Saliglau	0	0	0	0	0	0	0	0	0	0
Salix pulchra Cham.	Salipulc	0	0	0	7	0	0	0	0	2	3
Vaccinium uliginosum L.	Vacculig	0	0	0	0	0	0	0	0	0	0
Vaccinium vitis-idaea L.	Vaccviti	0	0	0	0	0	0	0	0	25	0
Forbs											
Petasites frigidus (L.) Fr.	Petafrig	0	0	0	0	0	0	0	0	0	0
Parrya nudicaulis (L.) Boiss.	Parrnudi	0	0	0	0	0	0	0	0	0	0
Pedicularis capitata Adams	Pedicapi	0	0	0	0	0	0	0	0	0	0
Pedicularis lapponica L.	Pedilapp	0	0	0	6	0	0	0	0	0	0
Pyrola grandiflora Radius	Pyrogran	0	0	0	0	0	0	0	0	0	0
Saxifraga nelsoniana D. Don	Saxinels	0	0	0	0	0	0	0	0	0	0
Valeriana capitata Pall. ex Link	Valecapi	0	0	0	0	0	0	0	0	0	0
Graminoids											
Arctagrostis latifolia (R.Br.) Griseb.	Arctlati	0	0	0	0	0	0	0	0	0	0
Calamagrostis holmii Lange	Calaholm	0	24	0	19	21	19	20	0	25	10
Carex aquatilis var. *minor* Boott	Careaqua	0	0	0	0	0	0	0	0	0	0
Carex bigelowii ssp. *arctisibirica* (Jurtzev) Á.& D.Löve	Carebige	0	0	0	0	0	0	0	0	0	0
Eriophorum angustifolium Honck.	Erioangu	25	0	25	0	0	1	0	25	0	0
Eriophorum vaginatum L.	Eriovagi	0	0	0	0	0	3	0	0	0	0
Luzula nivalis (Laest.) Spreng.	Luzuniva	0	0	0	0	0	0	0	0	0	0
Luzula wahlenbergii Rupr.	Luzuwahl	0	0	0	0	0	0	0	0	0	0
Bryophytes											
Aulacomnium palustre (Hedw.) Schwägr.	Aulapalu	0	5	0	0	0	0	0	0	3	1
Aulacomnium turgidum (Wahlenb.) Schwägr.	Aulaturg	0	19	0	23	16	0	4	0	6	17
Blepharostoma trichophyllum (L.) Dumort.	Bleptric	0	0	0	11	0	0	0	0	0	0
Brachythecium sp.	Bracsp	0	0	0	0	0	0	0	0	0	0
Dicranum elongatum Schleich. ex Schwägr.	Dicrelon	0	19	0	0	0	0	19	0	0	0
Dicranum spadiceum J.E. Zetterst	Dicrspad	0	19	0	16	21	25	0	0	20	17
Dicranum sp.	Dicrsp	0	0	0	0	0	0	0	0	0	0
Hylocomium splendens (Hedw.) Schimp.	Hylosple	0	0	0	0	0	0	0	0	0	0
Polytrichastrum alpinum (Hedw.) G.L. Sm.	Polyalpi	0	0	0	21	0	0	0	0	13	0
Polytrichum hyperboreum R. Br.	Polyhype	0	25	0	21	0	0	0	0	22	0
Polytrichum jensenii I. Hagen	Polyjens	0	0	0	0	0	0	0	0	0	0
Polytrichum juniperinum Hedw.	Polyjuni	0	25	0	0	12	23	25	0	15	16
Polytrichum piliferum Hedw.	Polypili	0	0	0	0	0	0	0	0	0	0

(continuation)

Species name	Abbr.	16	17	18	19	20	21	22	23	24	25
Bryophytes											
Ptilidium ciliare (L.) Hampe	Ptilcili	0	0	0	3	0	3	2	0	0	3
Sanionia uncinata (Hedw.) Loeske	Saniunci	0	0	0	0	0	0	0	0	0	0
Sphagnum balticum (Russow) C.E.O. Jensen	Sphabalt	0	0	0	0	0	0	0	0	0	0
Sphagnum compactum Lam. & DC.	Sphacomp	0	0	0	5	0	0	0	0	0	0
Sphagnum lenense Pohle	Sphalene	0	0	0	0	0	0	0	0	0	0
Sphagnum obtusum Warnst.	Sphaobtu	0	0	25	0	0	0	0	25	0	0
Sphagnum squarrosum Crome	Sphasqua	0	0	0	0	0	0	0	0	0	0
Sphagnum teres (Schimp.) Ångström	Sphatere	0	0	0	0	0	2	0	0	0	0
Sphenolobus minutus (Schreb.) Berggr.	Spheminu	0	19	0	16	24	25	20	0	18	17
Tomentypnum nitens (Hedw.) Loeske	Tomenite	0	0	0	0	0	0	0	0	0	0
Tritomaria exsectiformis (Breidl.) Schiffner ex Loeske	Tritexse	0	0	0	0	0	0	0	0	0	0
Lichens											
Alectoria nigricans (Ach.) Nyl	Alecnigr	0	0	0	0	0	0	0	0	0	0
Cetraria ericetorum Opiz	Cetreric	0	0	0	0	0	0	0	0	0	0
Cetraria islandica (L.) Ach.	Cetrisla	7	22	0	0	8	13	0	3	3	6
Cladonia amaurocraea (Florke) Schaerer	Cladamau	0	0	0	0	0	0	0	0	0	0
Cladonia borealis S. Stenroos	Cladbore	0	0	0	0	0	0	0	0	0	0
Cladonia cenotea (Ach.) Schaerer	Cladceno	0	0	0	0	0	0	0	0	0	0
Cladonia chlorophaea (Florke ex Sommerf.) Sprengel	Cladchlo	0	0	0	0	0	0	0	0	0	0
Cladonia coccifera (L.) Willd.	Cladcocc	0	0	0	0	0	0	0	0	0	0
Cladonia cornuta (L.) Hoffm.	Cladcorn	0	0	0	0	0	0	0	0	0	0
Cladonia cyanipes (Sommerf.) Nyl.	Cladcyan	0	0	0	0	0	0	0	0	0	0
Cladonia deformis (L.) Hoffm.	Claddefo	2	0	0	0	0	0	0	0	0	0
Cladonia ecmocyna Leighton	Cladecmo	0	0	0	0	0	0	0	0	0	0
Cladonia gracilis (L.) Willd.	Cladgrac	4	1	0	0	0	0	0	4	0	0
Cladonia macroceras (Delise) Hav.	Cladmacr	0	0	0	0	0	0	0	0	0	0
Cladonia pleurota (Florke) Schaerer	Cladpleu	0	0	0	0	0	0	0	0	0	0
Cladonia rangiferina (L.) F. H. Wigg.	Cladrang	0	0	0	0	0	0	0	0	0	0
Cladonia sulphurina (Michaux) Fr.	Cladsulp	0	0	0	0	0	0	0	0	0	0
Dactylina arctica (Richardson) Nyl.	Dactarct	0	0	0	0	0	0	0	0	0	0
Flavocetraria cucullata (Bellardi) Karnefelt & Thell	Flavcucu	25	25	0	0	23	25	0	24	6	5
*Nephroma expallidum (*Nyl.) Nyl.	Nephexpa	0	0	0	0	0	0	0	0	0	0
Ochrolechia inaequatula (Nyl.) Zahlbr.	Ochrinae	0	0	0	0	0	0	0	0	0	0
Peltigera aphtosa (L.) Willd.	Peltapht	0	0	0	0	0	4	1	0	10	1
Peltigera frippii Holt.-Hartw.	Peltfrip	0	0	0	0	0	0	0	0	0	0
Peltigera leucophlebia (Nyl.) Gyelnik	Peltleuc	0	0	0	0	0	0	0	0	0	0
Peltigera occidentalis (Å.E. Dahl) Kristinsson	Peltocci	0	1	0	0	0	0	0	0	0	0
Peltigera scabrosa Th. Fr.	Peltscab	0	0	0	0	0	0	0	0	0	0
Protopannaria pezizoides (Weber) Joerg & Ekman	Protpezi	0	0	0	0	0	0	0	0	0	0
Stereocaulon alpinum Laurer ex Funck	Steralpi	0	0	1	0	0	0	0	0	0	0
Thamnolia vermicularis (Sw.) Ach. ex Schaerer	Thamverm	0	0	0	0	0	0	0	0	0	3

Table A2.2b: Species name including authority, abbreviation, and abundance on the lakebed plots (P26-30, P36-40).

Species name	Abbr.	26	27	28	29	30	36	37	38	39	40
Shrubs											
Arctous alpina (L.) Nied.	Arctalpi	0	0	0	0	0	0	0	0	0	0
Betula nana ssp. *exilis* (Sukazcev) Hultén	Betunana	21	19	0	12	23	12	13	21	22	25
Cassiope tetragona (L.) D. Don.	Casstetr	0	0	0	0	0	0	0	0	0	0
Dryas octopetala L.	Dryaocto	0	0	0	0	0	0	0	0	0	0
Ledum palustre ssp. *decumbens* (Aiton) Hultén	Ledupalu	0	4	0	0	0	0	0	12	0	0
Salix fuscenses Andersson	Salifusc	0	0	5	0	0	0	13	0	0	0
Salix glauca L.	Saliglau	0	0	0	0	0	0	0	0	0	0
Salix pulchra Cham.	Salipulc	0	0	14	11	1	1	3	0	12	6
Vaccinium uliginosum L.	Vacculig	0	0	0	0	0	0	0	0	0	0
Vaccinium vitis-idaea L.	Vaccviti	0	25	0	8	0	25	0	25	25	18
Forbs											
Petasites frigidus (L.) Fr.	Petafrig	0	0	0	0	0	0	0	0	0	0
Parrya nudicaulis (L.) Boiss.	Parrnudi	0	0	0	0	0	0	0	0	0	0
Pedicularis capitata Adams	Pedicapi	0	0	0	0	0	0	0	0	0	0
Pedicularis lapponica L.	Pedilapp	0	0	0	0	0	0	0	0	1	12
Pyrola grandiflora Radius	Pyrogran	0	0	0	0	0	0	0	0	0	0
Saxifraga nelsoniana D. Don	Saxinels	0	0	8	0	0	0	0	0	0	0
Valeriana capitata Pall. ex Link	Valecapi	0	0	0	0	0	0	0	0	0	0
Graminoids											
Arctagrostis latifolia (R.Br.) Griseb.	Arctlati	0	9	0	0	0	6	0	0	0	0
Calamagrostis holmii Lange	Calaholm	6	17	2	5	0	8	5	16	23	3
Carex aquatilis var. *minor* Boott	Careaqua	0	0	8	18	0	0	0	0	12	0
Carex bigelowii ssp. *arctisibirica* (Jurtzev) Á.& D.Löve	Carebige	0	0	0	0	0	0	0	0	0	0
Eriophorum angustifolium Honck.	Erioangu	0	0	25	8	18	0	23	0	0	19
Eriophorum vaginatum L.	Eriovagi	0	2	0	1	1	0	0	0	0	0
Luzula nivalis (Laest.) Spreng.	Luzuniva	0	0	0	0	0	0	0	0	0	0
Luzula wahlenbergii Rupr.	Luzuwahl	0	0	0	2	0	0	0	0	0	0
Bryophytes											
Aulacomnium palustre (Hedw.) Schwägr.	Aulapalu	0	0	21	3	0	0	0	0	0	0
Aulacomnium turgidum (Wahlenb.) Schwägr.	Aulaturg	11	2	0	0	6	22	20	5	8	9
Blepharostoma trichophyllum (L.) Dumort.	Bleptric	0	0	0	0	0	0	0	0	0	0
Brachythecium sp.	Bracsp	0	0	0	0	0	0	0	0	0	0
Dicranum elongatum Schleich. ex Schwägr.	Dicrelon	0	23	0	0	0	0	0	0	0	0
Dicranum spadiceum J.E. Zetterst	Dicrspad	23	23	0	1	21	0	0	0	0	0
Dicranum sp.	Dicrsp	0	0	0	0	0	18	22	11	16	25
Hylocomium splendens (Hedw.) Schimp.	Hylosple	0	0	0	0	0	0	0	0	0	0
Polytrichastrum alpinum (Hedw.) G.L. Sm.	Polyalpi	0	0	0	4	0	0	0	0	0	0
Polytrichum hyperboreum R. Br.	Polyhype	0	0	0	0	0	0	0	0	0	0
Polytrichum jensenii I. Hagen	Polyjens	0	0	10	0	0	0	0	0	0	0
Polytrichum juniperinum Hedw.	Polyjuni	16	10	0	0	23	0	0	0	0	0
Polytrichum piliferum Hedw.	Polypili	0	0	0	0	0	0	0	0	0	0

(continuation)

Species name	Abbr.	26	27	28	29	30	36	37	38	39	40
Bryophytes											
Ptilidium ciliare (L.) Hampe	Ptilcili	3	0	0	0	0	0	0	7	0	14
Sanionia uncinata (Hedw.) Loeske	Saniunci	0	0	0	0	0	0	0	0	0	0
Sphagnum balticum (Russow) C.E.O. Jensen	Sphabalt	0	0	0	0	0	0	0	0	0	0
Sphagnum compactum Lam. & DC.	Sphacomp	0	0	0	0	0	0	0	0	0	0
Sphagnum lenense Pohle	Sphalene	0	0	0	0	0	0	0	0	0	0
Sphagnum obtusum Warnst.	Sphaobtu	0	0	10	25	0	0	15	0	23	18
Sphagnum squarrosum Crome	Sphasqua	0	0	0	0	0	0	0	0	0	0
Sphagnum teres (Schimp.) Ångström	Sphatere	0	0	0	0	0	0	0	0	0	0
Sphenolobus minutus (Schreb.) Berggr.	Spheminu	23	23	0	1	21	18	17	9	23	25
Tomentypnum nitens (Hedw.) Loeske	Tomenite	0	0	0	0	0	20	0	22	25	5
Tritomaria exsectiformis (Breidl.) Schiffner ex Loeske	Tritexse	0	0	0	2	0	0	0	0	0	0
Lichens											
Alectoria nigricans (Ach.) Nyl	Alecnigr	0	0	0	0	0	0	0	0	0	0
Cetraria ericetorum Opiz	Cetreric	0	0	0	0	0	0	0	0	0	0
Cetraria islandica (L.) Ach.	Cetrisla	7	22	0	0	8	13	0	3	3	6
Cladonia amaurocraea (Florke) Schaerer	Cladamau	0	0	0	0	0	0	0	0	0	0
Cladonia borealis S. Stenroos	Cladbore	0	0	0	0	0	0	0	0	0	0
Cladonia cenotea (Ach.) Schaerer	Cladceno	0	0	0	0	0	0	0	0	0	0
Cladonia chlorophaea (Florke ex Sommerf.) Sprengel	Cladchlo	0	0	0	0	0	0	0	0	0	0
Cladonia coccifera (L.) Willd.	Cladcocc	0	0	0	0	0	0	0	0	0	0
Cladonia cornuta (L.) Hoffm.	Cladcorn	0	0	0	0	0	0	0	0	0	0
Cladonia cyanipes (Sommerf.) Nyl.	Cladcyan	0	0	0	0	0	0	0	0	0	0
Cladonia deformis (L.) Hoffm.	Claddefo	2	0	0	0	0	0	0	0	0	0
Cladonia ecmocyna Leighton	Cladecmo	0	0	0	0	0	0	0	0	0	0
Cladonia gracilis (L.) Willd.	Cladgrac	4	1	0	0	0	0	0	4	0	0
Cladonia macroceras (Delise) Hav.	Cladmacr	0	0	0	0	0	0	0	0	0	0
Cladonia pleurota (Florke) Schaerer	Cladpleu	0	0	0	0	0	0	0	0	0	0
Cladonia rangiferina (L.) F. H. Wigg.	Cladrang	0	0	0	0	0	0	0	0	0	0
Cladonia sulphurina (Michaux) Fr.	Cladsulp	0	0	0	0	0	0	0	0	0	0
Dactylina arctica (Richardson) Nyl.	Dactarct	0	0	0	0	0	0	0	0	0	0
Flavocetraria cucullata (Bellardi) Karnefelt & Thell	Flavcucu	25	25	0	0	23	25	0	24	6	5
*Nephroma expallidum (*Nyl.) Nyl.	Nephexpa	0	0	0	0	0	0	0	0	0	0
Ochrolechia inaequatula (Nyl.) Zahlbr.	Ochrinae	0	0	0	0	0	0	0	0	0	0
Peltigera aphtosa (L.) Willd.	Peltapht	0	0	0	0	0	4	1	0	10	1
Peltigera frippii Holt.-Hartw.	Peltfrip	0	0	0	0	0	0	0	0	0	0
Peltigera leucophlebia (Nyl.) Gyelnik	Peltleuc	0	0	0	0	0	0	0	0	0	0
Peltigera occidentalis (Å.E. Dahl) Kristinsson	Peltocci	0	1	0	0	0	0	0	0	0	0
Peltigera scabrosa Th. Fr.	Peltscab	0	0	0	0	0	0	0	0	0	0
Protopannaria pezizoides (Weber) Joerg.& Ekman	Protpezi	0	0	0	0	0	0	0	0	0	0
Stereocaulon alpinum Laurer ex Funck	Steralpi	0	0	1	0	0	0	0	0	0	0
Thamnolia vermicularis (Sw.) Ach. ex Schaerer	Thamverm	0	0	0	0	0	0	0	0	0	3

Appendix 3: Local flora of the study area (Kytalyk)

In collaboration with O.V. Khitun *(Komarov Botanical Institute, Russian Academy of Science, St. Petersburg, Russia).*

Introduction

The local flora method was introduced by Tolmachev (1931), who proposed that a minimal natural floristic entity can be distinguished in the field and compared with other floristic units. This method has been used by Russian botanists for studying various bioclimatic zones (Baranova 1994; Bubyreva 1997; Yurtsev 2004). The method consists in identifying all the vascular plant species present in a specific area. This area must be big enough to reveal all possible habitats types, but small enough so species occurrence is determined by local environmental factors and not by geographic or climatic differences (e.g. 100 km^2 in arctic lowlands).

Local floras provide comparable data for temporal and spatial comparisons of plant distribution at the same and different locations. Thereby, the local flora method can be applied for monitoring vascular plant diversity and identifying rare species and spatial species patterns (Khitun *et al.* 2016).

Methodology

The study area was located in the Kytalyk nature reserve (see Chapter 1), at the bank of the Berelech river, which is a tributary of the Indigirka river. We explored the area around the research station (70° 49' N, 147° 28' E) by radial routes about 5-6 km long from 8th to 19th July 2013 (ca. 100 km^2). We compiled species lists for all existing habitat types in the area (Fig. A3.1). In addition, we recorded species abundance (visual cover estimation using the extended Braun-Blanquet scale (van der Maarel 1979) and their frequency of occurrence (rare, sparse, or common). Voucher specimens were collected of all species to make the herbarium of the local flora and to determine species in the laboratory when the field determination was in doubt. Furthermore, we measured *in situ* soil temperature, soil pH, and active layer thickness, and extracted soil profiles to estimate the thickness of the different layers (from moss layer to permafrost). Soil samples of the profiles were taken to estimate bulk density, carbon to nitrogen ratio, and cellulose to lignin ratio (data not shown).

Results

In the surroundings of the research station, 12 habitats were distinguished (Table A3.1). Within these habitats, 133 vascular plant species belonging to 68 genera and 28 families were found. In the following, some examples of these findings are described. Tussock tundra occupied the relatively drained yedoma hill present in the area (mainly, *Eriophorum vaginatum, Ledum palustre, Betula nana, Salix pulchra, Calamagrostis holmii*). Ericoid dwarf shrub dominated tundra with well-developed moss cover was found on the southern slope of the yedoma hill (7-10° steep) and pingos (*L. palustre, Vaccinium uliginosum, V. vitis-idaea, Arctous alpina, Empetrum nigrum, Pyrola grandiflora, Pedicularis capitata, Saxifraga nelsoniana, Persicaria bistorta, Valeriana capitata).* Pioneer herbaceous-grass dominated eroded steep parts of the river bank and the yedoma hill (*Calamagrostis arundinacea, Puccinellia borealis, Equisetum arvense, Descurainia sophioides, Draba juvenilis*) (Fig. A3.1). Shrub willow thickets, which reached 2.5 m in height, densely covered parts of the flood plain nearest to the river bed (*S. pulchra, S. lanata).*

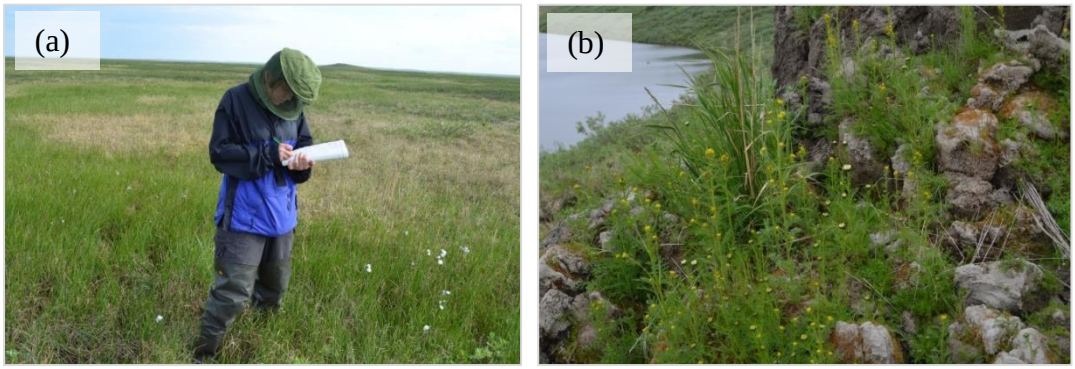

Figure A3.1. Relevé data collection (a); grass-herbaceous groupings on eroded dry ground (b).

The vascular species richness was lower than in analogous habitat types distinguished in the West Siberian Arctic (see Table A3.1). However, the composition of most diverse families was similar when comparing Kytalyk with other local floras from the low Indigirka area (results not shown). The most diverse families were *Poaceae* (16 species) > *Cyperaceae* (15 species) > *Caryophyllaceae* = *Salicaceae* (10 species each) > *Brassicaceae* (9 species) > *Saxifragaceae* = *Ranunculaceae* = *Scrophulariaceae* (8 species each) > *Asteraceae* = *Juncaceae* = *Ericaceae* (6 species each). The Kytalyk local flora differs from neighbouring floras by the absence of the families *Fabaceae, Lycopodiaceae,* and *Genianaceae.*

Table A3.1: Comparison of species richness of various habitat types in Kytalyk and theTazovsky peninsula.

Habitat	Number of species	
	Kytalyk	Tazovsky (in Khitun 1998)
Top and gentle slopes of the yedoma hill	31	34-49
Polygons of the high-centred polygonal tundra-mire complexes	21	25-30
Oligotrophic wet troughs of polygonal complexes	10	16-20
'Ridges' of low centred polygonal complexes	32	Absent
Eutrophic troughs, mires (alas depression in Kytalyk)	28	32-52
Short steep slopes (10-15 m) (yedoma hill in Kytalyk)	39	45-70
Long steep slopes (20-30 m) (pingos in Kytalyk)	47	53-69
Eroded drained bank of the river	39	33-51
Depressions with water flow between lakes	41	43-44
Floodplain (willow thickets on river terrace)	25	51-54
Snowbeds at hill foots (yedoma hill and pingos in Kytalyk)	30	61-69
Aquatic habitats (lakes)	12	17

Moreover, few rare species were found in the study area (*Alnus fruticosa, Moehringia lateriflora, Orthilia obtusata, Pedicularis penelli, Polygonum tripterocarpum, Salix myrtilloides, Triglochin maritimum, Utricularia intermedia, Utricularia minor).*

Discussion

The Kytalyk local flora has all typical features of the region and is representative for vast lowland areas in the low Indigirka. However, the number of vascular plant species found in Kytalyk is very poor for a Yakutian local flora (Boch & Tsaryova 1974; Egorova *et al.* 1991). This lower richness may be attributed to a smaller number of habitats (12) compared with other regions (e.g. West Siberian Arctic (15-22; Khitun 1998)), especially to the scarcity of short and long steep slopes, which are the richest habitats in Siberia (only two pingos and one yedoma hill were present in the vicinity of the Kytalyk research station). Furthermore, the almost absence of drained slopes may explain the smaller number of species in all leading families, especially the families *Poaceae, Cyperaceae,* and *Asteraceae.*

Although there were some floristic surveys along the Indigirka river, the local flora presented here is the first one in this area (Boch & Tsaryova 1974). In the Indigirka surveys, only 155 species were found initially (Boch & Tsaryova 1974), though new species were added during later surveys (30 species, Egorova *et al.* 1991), reaching approximately 220 species vascular

plant species in a preliminary checklist by T.M. Koroleva and P.A. Gogoleva (2013, personal communication). These changes in the number of species suggest that some of the rare species found in the area were likely not found in the previous surveys, but also may indicate a species expansion northwards, implying new northernmost locations of some hypoarctic and boreal species.

The local flora method provides information about spatial distribution and differentiation of species diversity at local and regional scales (Khitun *et al.* 2016). Moreover, documented species diversity and distribution of tundra vegetation in local floras may provide species diversity baselines for different regions (Walker *et al.* 2013). These baselines may be compared temporally and spatially, at one or several locations, to provide insight on arctic species vulnerability (e.g. species migration, shifts in species abundance) to climate change.

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Appendix 4: Soil temperature profile of the experimental plots

Soil temperature was continuously measured at four depths in all the experimental plots (Chapters 3 and 4) using temperature loggers (iButton DS1922L/DS1921G, Maxim Integrated, USA). All temperature loggers, except eight missing ones, were recovered the last year of experiment to extract the recorded data (Table A4.1). Heated cables increased significantly soil temperature by 1.0°C, but only at 15 and 25 cm depth during the growing season ($F_{1, 21} = 16.2$, $P < 0.01$; $F_{1, 21} = 13.0$, $P < 0.01$).

Table A4.1: Mean soil temperature (standard deviation) of the five experimental blocks for each treatment combination (no-cable (Ct), unheated cable (Ca), heated cable (W), no nutrient addition (NF), and nutrient addition (F)). Temperature is expressed in degrees Celsius.

	CtNF	CaNF	WNF	CtF	CaF	WF
Annual						
0 cm	-7.6 (11.6)	-7.5 (11.6)	-6.8 (10.7)	-7.8 (11.2)	-7.9 (11.1)	-6.8 (10.6)
5 cm	-7.6 (9.6)	-7.6 (9.8)	-6.5 (9.2)	-7.9 (9.1)	-7.8 (9.3)	-6.6 (9.0)
15 cm	-7.8 (8.0)	-7.8 (8.3)	-6.6 (8.0)	-8.0 (7.7)	-7.9 (7.9)	-6.7 (7.8)
25 cm	-7.7 (7.4)	-7.8 (7.8)	-6.7 (7.5)	-8.0 (7.4)	-7.8 (7.5)	-6.8 (7.3)
Growing season (June – August)						
0 cm	+8.9 (2.0)	+8.7 (2.2)	+8.8 (2.3)	+7.9 (1.8)	+7.9 (1.8)	+8.0 (2.0)
5 cm	+5.2 (1.9)	+5.4 (2.3)	+5.5 (2.1)	+3.8 (1.6)	+4.3 (1.9)	+5.0 (1.9)
15 cm	+1.6 (1.2)	+2.1 (1.7)	+2.7 (1.8)	+0.7 (1.2)	+1.3 (1.4)	+2.1 (1.5)
25 cm	+0.3 (1.0)	+0.9 (1.5)	+1.4 (1.6)	-0.1 (1.1)	+0.3 (1.2)	+1.0 (1.4)
No-growing season (September – May)						
0 cm	-13.1 (7.4)	-12.9 (7.4)	-11.6 (7.1)	-13.1 (7.2)	-13.1 (7.1)	-11.7 (7.0)
5 cm	-11.8 (6.9)	-11.9 (7.1)	-10.5 (6.8)	-11.8 (6.8)	-11.8 (6.9)	-10.4 (6.7)
15 cm	-10.9 (6.7)	-11.1 (6.9)	-9.7 (6.7)	-10.9 (6.7)	-10.9 (6.7)	-9.6 (6.7)
25 cm	-10.4 (6.6)	-10.7 (6.8)	-9.5 (6.6)	-10.6 (6.6)	-10.6 (6.6)	-9.4 (6.5)

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Publications

Iturrate-Garcia, M., O'Brien, M.J., Khitun, O., Abiven, S., Niklaus, P.A. & Schaepman-Strub, G. (2016) Interactive effects between plant functional types and soil factors on tundra species diversity and community composition. *Ecology and Evolutio*n, **6**, 81267–8137, doi: 10.1002/ ece3.2548.

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Iturrate-Garcia, M., Heijmans, M.M.P.D., Schweingruber, F.H., Niklaus, P.A. & Schaepman-Strub, G. "Soil warming and fertilization effects on growth ring widths of arctic shrubs", American Geophysics Union Fall Meeting, December 2015, San Francisco, USA (poster).

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International Symposium C/H_2O/energy balance and climate over the boreal and Arctic regions with special emphasis on Eastern Eurasia, November 2016, Yakustk, Russian Federation (oral).

Seminars

Iturrate-Garcia, M. "Arctic vegetation effects on the radiation balance", Spectroscopy Seminar, October 2015, Greifensee, Switzerland (oral).

Iturrate-Garcia, M. "Do vegetation communities matter in a changing Arctic?", Behaviour, Ecology, Environment and Evolution Seminar **(**BEEES), November 2015, Zurich, Switzerland (oral).

Courses

Subject-specific matters

Arctic species determination and community associations	2 ECTS
ECO 301 Journal club	1 ECTS
ECO 339 Community Ecology	1 ECTS

Methods

Study design and data analysis using the statistical software R-1	2 ECTS
ECO 302 Scientific writing	1 ECTS
ECO 332 R4All. A recipe for success with R	1 ECTS
ECO 334 Mixed-effects modelling with ASReml	2 ECTS

Transferable skills

Voice training and presentation skills in the Sciences and Medicine	1 ECTS
Speaking with confidence and impact	1 ECTS
ECO 364 Introduction to teaching field practica	1 ECTS

Research seminars

Global Vegetation Monitoring and Modeling, Avignon, France (poster)	1 ECTS
C/H_2O/Energy balance and climate over boreal and arctic regions with special emphasis on eastern Eurasia, Wageningen, the Netherlands (oral)	1 ECTS

Other

ECO 367 First aid training: far from help	1 ECTS

Total: 16 ECTS

Teaching

BIO 141 Oekologie und Biodiversität (Praktikum)	8 hours
BIO 141 Oekologie und Biodiversität (Praktikum)	8 hours
UWW 271 Contemporary analysis for ecology	9 hours
UWW 252 Spatial ecology and remote sensing	72 hours
Master student supervising	50 hours

Student: Rachel Simeon

Thesis title: The effects of nutrient addition and soil warming on Arctic shrubs in Northeastern Siberia.

Total: 147 hours

It is time to give thanks to all the people who made possible this project, directly or indirectly. Please, be aware that the order of appearance is not necessarily correlated with the importance of the contributions.

This long, long journey started in April 2008, when I got a position as a research assistant in the Centre for Environmental Studies of the Mediterranean (CEAM, Valencia, Spain). The task was easy: classify the biomass collected in different eddy-covariance test sites into green and dry biomass. While classifying (quite a boring task), I kept listening all the conversations around to learn more about terrestrial ecosystems. Finally, after one year of "arguments" and why- questions, and showing that the methods I was forced to use were not the best, my former boss, Arnaud Carrara, offered me the opportunity to start a PhD under his direction. To convince me, he told me one sentence that I will never forget: "You are not brilliant and not very fast learning, but you have three skills that will make you a suitable doctoral candidate: you are hard-working, enthusiastic and inquisitive" (thanks, Arnaud). I would like to extent the thanks to all members of the research group Effects of Pollutants in Vegetation and especially to the CO_2 group. Special thanks go to Cristina Gimeno Cólera for her advice and supervision during my master thesis, Jose Vicente Chordá Sancho for the interesting research discussions (and the mandarins!!) and Agustí Palomares Palacios for sharing hard times in the field and making them softer.

Unfortunately, the financial crisis struck Spain and the research funding was cut. After one year and a half of doctoral studies, I had to start searching for a new PhD position. In this search and when I was about to throw in the towel, I found an advertisement that caught my eye: "[...] the field work will take place in Siberia under very basic life conditions". This was the perfect opportunity to run away from the heat of the Mediterranean ecosystems (yes, incredible to believe, but I hate warm places). So, I applied two days before the deadline and, to my surprise, I was invited for an interview in October 2012 in Zurich (due to Skype communication problems during the first interview). Here, I'd like to thank my supervisors Gabriela Schaepman-Strub and Pascal A. Niklaus for believing in me that day and give me the opportunity of joining this great adventure. I would also like to thank them for their advice and for telling me the magic words: "this is your project", as well as, how not, the many nights without sleeping (side effects of this doctoral project). Special thanks also go to my other committee members (Bernhard Schmid, Owen Petchey and Monique Heijmans) for

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